DIET OF THE SANDBAR SHARK, *CARCHARHINUS PLUMBEUS*, IN CHESAPEAKE BAY AND ADJACENT WATERS

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Julia K. Ellis

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Julia K. Ellis

Julia K. Ellis

Approved, June 2003

John A. Musick

John A. Musick, Ph.D.
Committee Chairman/Advisor

Herbert M. Austin

Herbert M. Austin, Ph.D.

Enric Cortés

Enric Cortés, PhD.
NOAA/NMFS Panama City Laboratory
Panama City, Florida

David A. Evans

David A. Evans, Ph.D.

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ABSTRACT

The sandbar shark, *Carcharhinus plumbeus*, is the most abundant large coastal shark in the temperate and tropical waters of the northwest Atlantic Ocean. The Chesapeake Bay, Virginia and adjacent waters serve as a nursery ground for *C. plumbeus* as well as many other fauna. Characterizing the diet of a higher trophic level predator such as the sandbar shark sheds light on a small portion of the temporally and spatially complex food web in the Bay. This study describes the diet of the sandbar shark, highlighting differences in diet within various portions of the nursery area, as well as ontogenetic changes in diet.

Stomach samples were obtained in 2001 and 2002 from 232 sharks caught in gillnets or by longline gear. Historical data from the Virginia Institute of Marine Science (VIMS) Shark Ecology program were also analyzed. Ontogenetic changes in diet were evident, with crustacean prey decreasing in importance and frequency with increasing shark size, and elasmobranch prey importance and frequency increasing with increasing shark size. While previous research in Chincoteague Bay, VA showed the blue crab, *Callinectes sapidus*, as the dominant crustacean in sandbar shark diet, the mantis shrimp, *Squilla empusa*, dominated the crustacean portion of the diet in this study.

Differences in diet were mainly attributable to location of shark capture. Small juveniles (< 80 cm precaudal length) in the lower Chesapeake Bay ate significantly more fishes, whereas Eastern Shore juveniles ate more crustaceans. The type of crustacean consumed varied within areas of the Eastern Shore, with more portunid crabs consumed in waters near Wachapreague and more mantis shrimp consumed near Sand Shoal Inlet. This study was not able to detect any change in diet over time due to insufficient sample sizes and the effect of location.

DIET OF THE SANDBAR SHARK, *CARCHARHINUS PLUMBEUS*, IN CHESAPEAKE BAY AND ADJACENT WATERS

INTRODUCTION

As the most abundant large coastal shark in the temperate and tropical waters of the northwest Atlantic Ocean, the sandbar shark, *Carcharhinus plumbeus,* is a top predator affecting many species in the food web. In the northwest Atlantic, *C. plumbeus* reaches maximum total lengths (TLs) of 234 cm (females) and 226 cm (males) and inhabits a range from southern New England to southern Florida and the Gulf of Mexico (Bigelow and Schroeder 1948; Springer 1960; Compagno 1984; Castro 1983; Sminkey and Musick 1995).

Within this range, the sandbar shark undertakes seasonal migrations to and from summer feeding and nursery grounds (Springer 1960; Musick and Colvocoressess 1986). The Chesapeake Bay is considered the primary nursery ground for this population (Musick and Colvocoressess 1986). In late May to early June, adult females (greater than 180 cm TL) migrate north and enter the Chesapeake Bay and inlets and bays along Virginia's Eastern Shore (among other bays and estuaries north to Cape Cod) to pup (Springer 1960; Musick and Colvocoressess 1986). Juveniles of both sexes return to nursery grounds during the summer, while adult males inhabit offshore waters south of Cape Hatteras. From June to August, females give birth to litters of 6 to 13 pups that measure between 45 and 50 cm precaudal length (PCL) (Springer

1960; Compagno 1984). After pupping, postpartum females migrate offshore to depths of 21 to 40 m (Musick and Colvocoressess 1986). All ages of *C. plumbeus* leave the Bay in September and October as temperatures fall and photoperiod changes (Musick et al. 1985; Musick and Colvocoressess 1986; Grubbs 2001). Offshore waters of Florida and North Carolina serve as the wintering grounds for adults and juveniles, respectively, from November through April (Grubbs 2001).

While in Chesapeake Bay and adjacent waters, *C. plumbeus* fits into an extremely complex food web, comprised of many seasonal residents. During the course of a year, the Chesapeake Bay ecosystem contains approximately 3,000 animal and plant species (Murdy et al. 1997). The Bay is an estuarine system with complex physical and chemical dynamics (Murdy et al. 1997), and its food web varies spatially as well as temporally. The large activity space (110 km^2) (Grubbs 2001) of juvenile sandbar sharks indicates that sandbar shark predation impacts many species in various areas of the lower Bay. Previous diet studies and recent tracking studies indicate that sandbar sharks forage in the water column as well as on and near the benthos, preying on fish, mollusks, crustaceans, and other elasmobranchs (Bigelow and Schroeder 1948; Springer 1960; Clark and von Schmidt 1965; Grubbs 2001). Understanding linkages between predators and prey is an important component of ecosystem-based fishery management (NMFS 1999), enabling managers to model population trends of target species.

Trophic interactions may change with time and may be affected by fishing pressure (Alonso et al. 2002), making it necessary to periodically monitor them by conducting diet studies. Medved et al. (1985) found the blue crab, *Callinectes sapidus*, to be an important part of sandbar shark diet in Chincoteague Bay, Virginia. The blue crab population has declined since these data were collected in 1983, with Virginia landings decreasing by 37 percent (VMRC 2001). More recent studies in this region have not yet been conducted, so the importance of blue crab in the current diet is not known.

Diet may also differ between age classes of *C. plumbeus*, as it does in many sharks (Wetherbee and Cortés, in press). General trends for carcharhinid sharks and other larger sharks such as the sixgill shark (*Hexanchus griseus*) and the sevengill shark (*Notorynchus cepedianus*), include increased diversity of prey and increased occurrence of larger, more energy-rich prey items such as elasmobranchs and mammals with increasing shark size (Cortés and Gruber 1990; Ebert 1994; Lowe et al. 1996; Ebert 2002). As sharks grow larger and mature, their activity space encompasses a greater number of habitat types. In Florida and the Bahamas, lemon shark (*Negaprion brevirostris*) neonates and juveniles feed exclusively on flats, whereas adults forage in reef habitats in addition to the flats, capturing prey that inhabits deeper waters (Cortés and Gruber 1990). As sharks get larger, not only are they more likely to encounter a more diverse array of prey species, but they also have increased physical ability to capture prey (Lowe et al. 1996). For example, the epaulette shark (*Hemiscyllium ocellatum*) consumes softer prey when young, transitioning to hard-bodied crustaceans as it gets older. This change in diet is likely related to increased jaw size (Heupel and Bennet 1998). In Hawaiian waters, large prey items (sea turtles, elasmobranchs, and marine mammals) are only found in the stomachs of tiger sharks (*Galeocerdo cuvier*) that are greater than 230 cm TL; this shift to larger prey is most likely due to the increased hunting ability and faster swimming capabilities of these larger animals (Lowe et al. 1996). Examining changes in diet with size and age can reveal much about niche and trophic changes that may occur during ontogeny.

Ontogenetic shifts in the diet of the sandbar shark have been examined to a small extent, but previous studies have used either an extremely broad sampling range (Georges Bank to Cape Hatteras) or an extremely small one (Chincoteague Bay, Virginia). Other studies are merely descriptive or only contain a small number of samples. Existing quantitative data on stomach content analysis of *C. plumbeus* in Virginia waters is based on studies by Lawler (1976), Medved et al. (1985), and Stillwell and Kohler (1993). These data were collected in the 1970s and 1980s and concentrated on the frequency of prey items present in stomachs and daily ration, or the amount of food consumed, expressed on a daily basis. Lawler (1976) described the contents of 162 stomachs (100 of which were empty) and listed the percent occurrence of food items for sandbar sharks captured near the mouth of the Chesapeake Bay. Although the animals ranged in size from 54 to 179 cm total length (TL), the diet observations were not segregated by size class. In 1983, Medved et al. (1985) gathered 414 stomachs (74 were empty) using gillnets and rod and reel in Chincoteague Bay and examined digestion stage and frequency of occurrence of prey items. The size of sharks sampled in the data set ranged between 40 and 80 cm fork length (FL), which corresponds to animals between the ages of 0 and 4 years (Sminkey and Musick 1995). Medved et al.'s (1985) data indicated that the blue crab was present in 82.1% of the neonate and juvenile sandbar stomachs containing food, whereas Lawler noted a predominance of fish.

Stillwell and Kohler (1993) used data from shark fishing tournaments, commercial and research longline cruises from Cape Hatteras to Georges Bank, as well as rod and reel fishing in Chincoteague Bay to describe the diet of the sandbar shark for the east coast of the United States from 1972 to 1984. They examined prey item volume, number, and frequency of occurrence, and they compared diets between nearshore (caught at depths <100 m) and offshore (caught at depths >100 m) groups. These data were used to estimate daily ration and consumption rates. The tournament and longline data, which were divided into nearshore and offshore data sets, identified teleosts followed by elasmobranchs as the most important prey species by percent frequency and percent number. Sandbar shark diet differed significantly between nearshore and offshore subsets; cephalopods occurred more frequently in the offshore samples, and flatfish occurred more frequently in the nearshore samples. It should be noted, however, that only 53 of the 321 samples were caught offshore. Their diet analysis was not divided into size classes. The Chincoteague Bay subset consisted of stomachs from pups and juveniles with a mean FL of 55 cm. The Chincoteague data confirmed Medved et al.'s (1985) findings: crustaceans, specifically the blue crab, dominated the diet (frequency of occurrence = 75.5%). Although Stillwell and Kohler (1993) calculated percent frequency (%F), percent number (%N), and percent volume (%V), they did not calculate these values for broader taxonomic categories, so index of relative importance (IRI) values can only be extrapolated for each specific prey item listed in their report.

While information exists on sandbar shark diet, there are still gaps to be filled. Crustaceans dominated the diet of neonates and juveniles in Chincoteague Bay in 1983, but whether this dominance holds true in other areas of the nursery in Virginia waters is unknown. Whether or not the blue crab is still the dominant crustacean in sandbar shark diet has also yet to be determined. Additionally, there may be intermediate changes in diet that cannot be revealed by comparing Medved et al.'s (1985) neonate and juvenile and Stillwell and Kohler's (1993) nearshore and offshore samples. To address these uncertainties, this study proposed to revisit sandbar shark diet with the following objectives:

1. Describe the current diet of the sandbar shark in Chesapeake Bay and adjacent waters.
2. Examine how differences in age or size of sandbar sharks are reflected in their diet.

3. Determine whether there have been any changes in diet over time.

METHODS

Data Collection

Data for this study were obtained from two sources: 1) archival diet data from the VIMS Shark Ecology Program from 1974 to 1998, and 2) samples collected by gillnet and longline from 2001-2002.

Archival Data

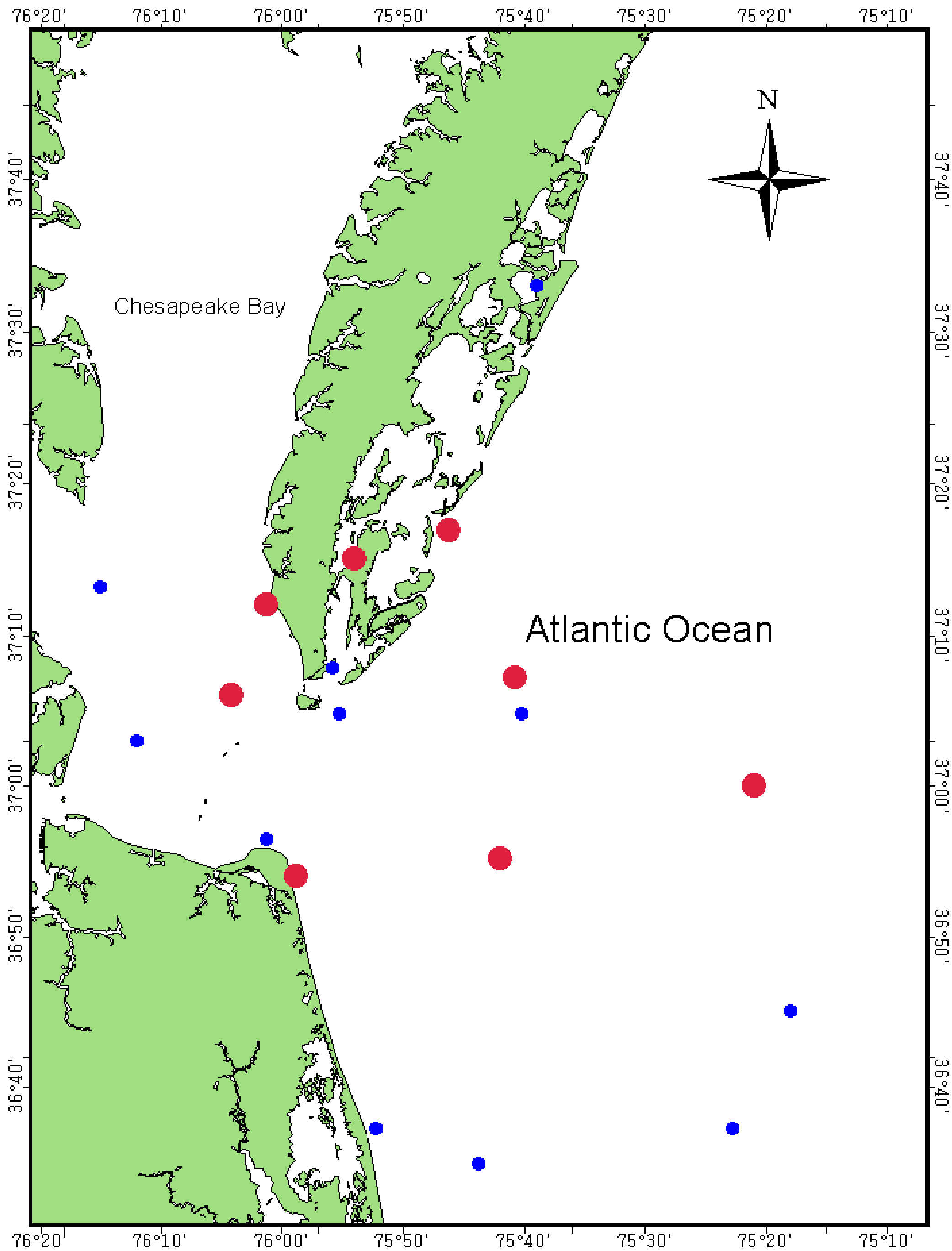
Stomach content data were collected sporadically on longline cruises from 1974 through 1998. Samples were collected by the staff of the VIMS Shark Ecology program, and breadth and frequency of stomach content examination were dependent on time constraints, funding, and sampling goals. Sharks were caught on a bottom-set longline composed of a tarred nylon mainline with 100 gangions spaced approximately 20 meters apart, buoys every 20 hooks, and anchors at both ends. For all sets, tuna “J” 9/0 hooks were used, but in the 1990s some 12/0 circle hooks were added to standard sets to include more small sharks and neonates in the catch. A standard set consisted of 100 hooks baited with locally available fish (usually Atlantic menhaden, *Brevoortia tyrannus*) cut into chunks, set for three to four hours. However, number of hooks ranged from 31 to 200 per set, and soak times ranged from 2 to 17 hours. Once landed, sandbar sharks set aside for sampling were sacrificed, and stomach contents were identified on board. Occasionally, weights and counts of individual prey items were also recorded. Results were recorded on data sheets which were kept on file. Sampling took place at various fixed and ancillary stations in Chesapeake Bay and adjacent waters (Figure 1). Ancillary sampling locations reflected changing project goals.

2001-2002 Study

Sandbar sharks were caught on standard longline sets from May through October 2001-2002. Animals were sacrificed and the stomachs were preserved in 10% formalin for analysis in the laboratory. Only the stomach portion of the digestive tract was excised due to the difficulty in identifying items further advanced in the digestion process (Berg 1979). Empty stomachs were discarded. Percentage of empty stomachs was not calculated because not all sharks caught were sacrificed. Total and precaudal lengths were measured to the nearest centimeter and recorded for all animals. Bite radius for both the upper and lower jaws was obtained by holding a string at the posterior-most tooth on one side of the jaw and running the string on the outside of the teeth to the posterior-most tooth on the other side. The length of string was then measured (P.J. Motta, pers. comm.).

Additional stomach samples were obtained using gillnets on Virginia's Eastern Shore monthly from May to October of 2002. Gillnets consisted of three 34-foot long, 8-foot tall panels of six-pound test monofilament in four-, five-, and six-inch stretched mesh buoyed at the top of the net with floats and weighted at the bottom with 50-pound leadcore. Four stations in each of three regions of Virginia's Eastern Shore (Wachapreague, Great Machipongo Channel, and Sand Shoal Inlet) were fished once a month for a total of twelve stations (Figure 2). Station location was adjusted as necessary if macroalgae or current strength became a problem. At each station, shallow (8-10 m) and deep (13-20 m) sites were selected, and a net

Figure 1: Map of fixed (red dots) and some ancillary (blue dots) longline stations of the VIMS Shark Ecology Program 1974-2002.



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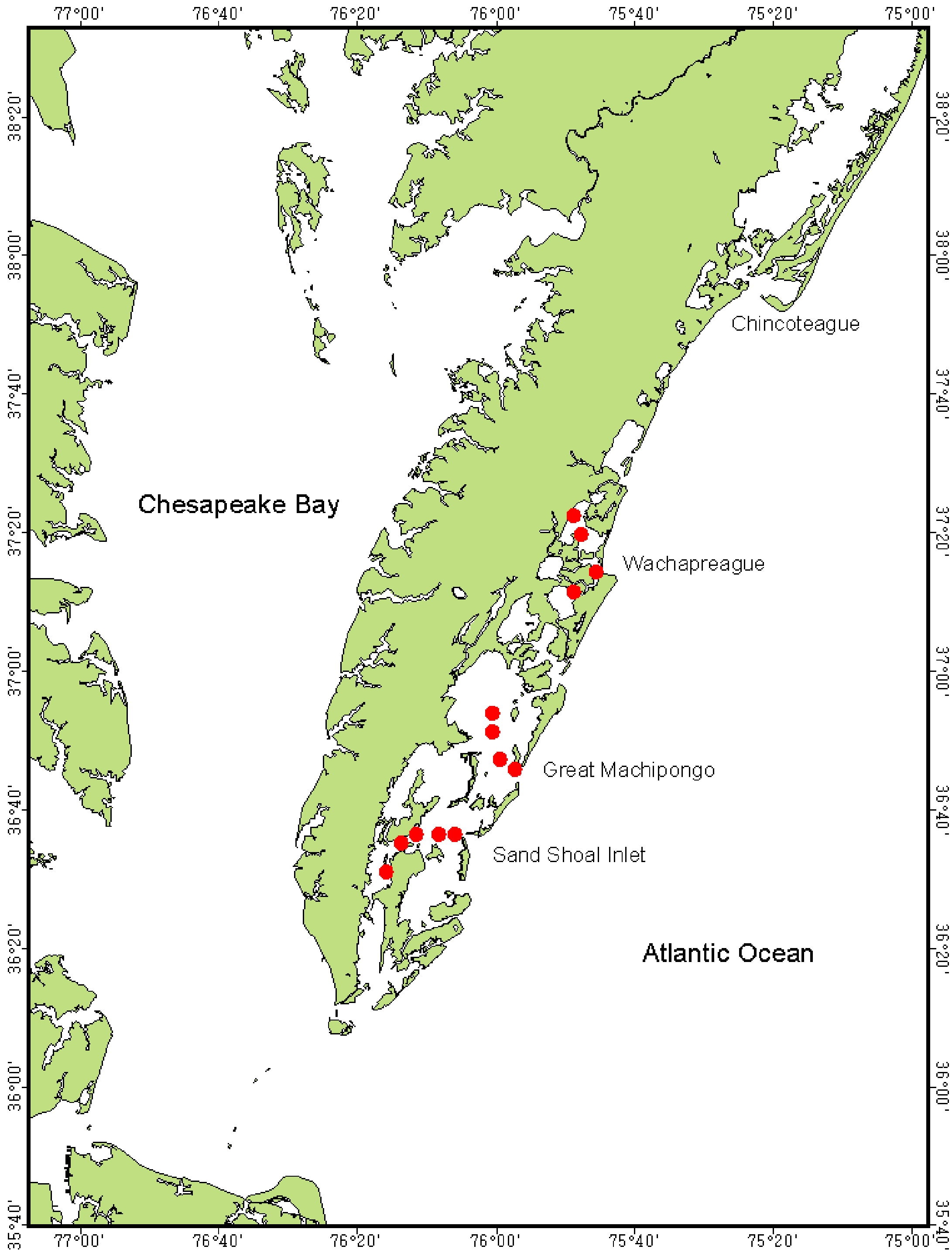
Chesapeake Bay
Atlantic Ocean

Figure 2: Map of gillnet sampling locations in 2002.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Chincoteague
Wachapreague
Great Machipongo
Sand Shoal Inlet
Atlantic Ocean

was set at each for one to one and a half hours. Total and precaudal lengths of all animals landed were measured, as was bite radius. Sharks were sacrificed and stomach samples were taken. The presence of empty stomachs was also recorded. Samples were stored on ice in plastic bags while in the field then frozen before being transferred to a 10% formalin solution. Samples were stored in formalin for at least 24 hours before analysis (Creaser and Perkins 1994).

Laboratory Analysis

Items in each stomach were sorted, identified to the lowest taxonomic level possible, and counted. Bait or secondary baits—animals eaten while hooked on the longline—were not counted or weighed. If bait or secondary bait was the only item in the stomach, the stomach was considered empty. If prey items were not whole or nearly whole, numbers were based on countable parts, such as claws and legs for crustaceans, otoliths for fishes, and beaks for cephalopods. After sorting and identification, prey items were rinsed with fresh water and blotted dry with a paper towel, then wet weights were measured to the nearest 0.1 g. Unidentifiable matter that could not be assigned to a particular prey item was labeled as unidentified and weighed separately. The samples were dried in an oven at 60 °C for 24 to 48 hours (Sturm and Horn 1998; Watanabe and Saito 1998). Dried stomach contents were weighed to the nearest tenth of a gram then stored in case future verification was required and/or new tools became available in identifying prey species.

Data Analysis

To assess the adequacy of the number of samples gathered, cumulative prey curves were constructed. The order in which the stomachs were examined was randomized using a random number generator in the Excel software package. Then the number of unique prey items was plotted against cumulative number of stomachs examined, following Ferry and Cailliet (1996). For each curve, the order of stomachs was randomized 10 times, and the mean number of unique prey items with standard deviation error bars was plotted to minimize bias resulting from sampling order (Ferry and Cailliet 1996; Gelsleichter et al. 1999). Cumulative prey curves were generated using family of prey species and were developed for both the entire data set, as well as subsets used in further analysis (Ferry et al. 1997). The use of cumulative prey curves is based on the assumption that if a curve reaches an asymptote, the diet has been adequately characterized because new prey types occur more and more infrequently. Cumulative prey curves can reflect sampling bias; for example, if all animals were captured at one location, the curve would be more likely to asymptote (Gartland 2002). On the other hand, animals collected in a variety of locations may have a wider variety of prey items which may affect the number of stomachs required to obtain an asymptote.

Common indices were used to describe the diet of the sandbar shark for the data obtained from the 2001-2002 samples and for subsets of that data set. Following Hyslop (1980), frequency of occurrence, number, and weight indices were calculated for each prey category. Frequency of occurrence (%F) was calculated by dividing the number of stomachs containing a particular prey item or category by the total number of stomachs containing prey multiplied by 100. This index reflects the number of predators which utilize that prey resource, or the homogeneity of the foraging strategy (Cortés 1997). Abundance (%N) was calculated by dividing the total number of prey items within the category by the total number of individual prey items multiplied by 100; this index can reflect abundance or size of prey. The gravimetric index (%W) was obtained by dividing the total weight of a prey category by the total weight of all prey items multiplied by 100. This index can reflect the energetic importance of a prey item. If regarded separately, each of these indices could reflect a bias toward highly abundant prey items (%F), very small prey items (%N), or very rare, large prey items (%W). Additionally, true importance of prey item weight is obscured by varying digestive rates (Pinkas et al. 1971). For these reasons, an index of relative importance (IRI) was calculated to determine the combined effect of these indices for each prey category. The formula for index of relative importance combines %N, %W, and %F as follows (Pinkas et al. 1971):

$$\mathrm{IRI} = (\%\mathrm{N} + \%\mathrm{W}) \times \%\mathrm{F}$$

Cortés (1997) recommended expressing the index of relative importance as a percentage for ease of comparison. Liao et al. (2001) confirmed that using %IRI provides a balanced general value of importance for a prey category. Percent IRI for n categories at given taxonomic levels was defined as:

$$\%\mathrm{IRI}_i = 100\,\mathrm{IRI}_i / \sum_{i=1}^{n} \mathrm{IRI}_i$$

Percent IRI values were calculated separately for both broad (e.g., teleosts, crustaceans, and elasmobranchs) and specific taxonomic categories of prey groups. Percent frequency values calculated for broad taxonomic prey groups were calculated separately due to the non-additive nature of frequency data (Cortés 1997). For example, a stomach containing two species of fish would only be counted once for the frequency of “fish”; however, adding the frequencies of all fish types would yield an artificially higher count.

Only one index, %F, was calculated for the data obtained from the archival data because of the paucity of weight and count information recorded. Weights that were recorded in the data sheets were measured with a different balance than the one used with the current samples, and in many cases, weights were measured in five-gram increments. Additionally, prey items examined onboard had not undergone preservation in formalin. Because formalin tends to increase prey item weight (DiStefano et al. 1994) and because the weights in the data sheets were measured by different people using different equipment, the weights recorded in the data sheets were not compared to those obtained from the 2001-2002 samples.

The Schoener and the Simplified Morisita indices of overlap were used to compare the similarity of diet between male and female sandbar sharks in the current data set. Prey items were grouped into broad categories: Teleostei, Crustacea, Elasmobranchii, Cephalopoda, and Unknown, which included unidentifiable prey items, as well as incidentally captured items such as plant matter. Following Wallace (1981), the fraction of wet weight a prey item contributed to the total wet weight of that stomach’s prey items was calculated for each stomach. Then the mean percent wet weight was calculated for each prey category. These values were used to calculate the Schoener index. As a precautionary measure against weight bias, %IRI was also used. The Schoener index (α) was then calculated as follows, where p_{ij} is the proportion of prey item i used by subgroup j, and p_{ik} is the proportion of prey item i used by subgroup k (Schoener 1970):

$$\alpha = 1 - 0.5(\sum|p_{ij}-p_{ik}|)$$

Values should range between zero and one, with those approaching one having the highest overlap.

Shark stomachs were grouped into four size classes based on precaudal lengths (PCLs): ≤ 60 cm, 61-80 cm, 81-100 cm, and > 100 cm. These groups were designated classes I, II, III, and IV, respectively. For the 2001-2002 data, %N, %F, %W, and %IRI were calculated for each size class for broad taxonomic categories: Teleostei, Crustacea, Elasmobranchii, Cephalopoda, Unknown, and Other. For the 2001-2002 data, the Schoener index of overlap was calculated for the size classes using average percent wet weight as previously described. The index was also calculated using %N, %F, %W, and %IRI. To verify these results, the Simplified Morisita index (C_H), which is commonly used in fish diet studies, was calculated:

$$C_H = 2(\sum p_{ij}p_{ik})/(\sum p^2_{ij} + \sum p^2_{ik})$$

where p_{ij} is the proportion of prey category i used by size class j, and p_{ik} is the proportion of prey category i used by size class k (Krebs 1989). Various indices, %IRI, %F, and %W, were used to calculate C_H. To further verify these results, the

Schoener and Simplified Morisita indices were calculated using %F values from the entire data set (archival and new data).

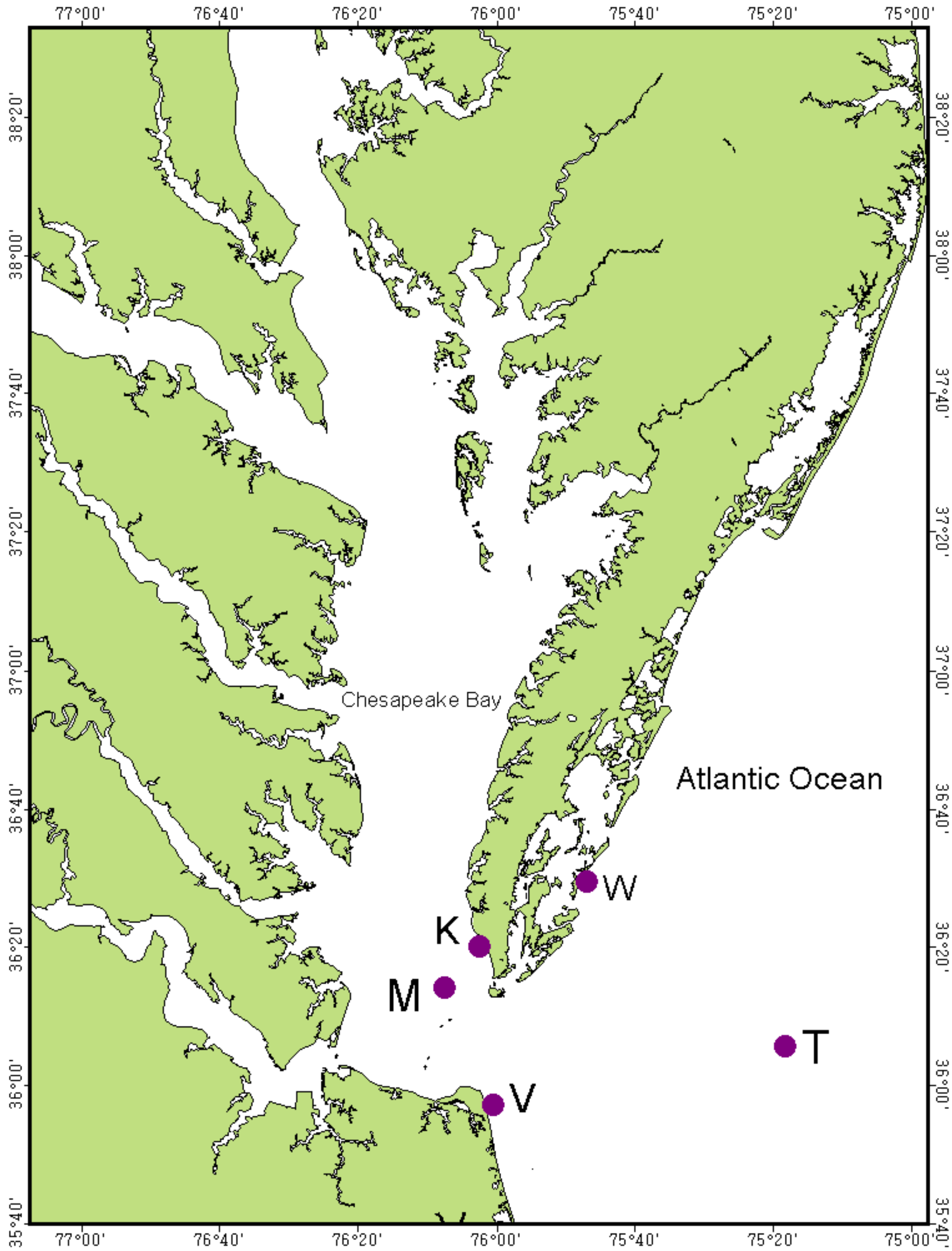
Prey diversity (H) was calculated using the Shannon-Wiener method. Percent frequency values from the entire data set were used in the following equation, where P_i is the contribution of prey category i to the diet (Zar 1996):

$$H = -\mathrm{sum}(P_i \log[P_i])$$

Simple correspondence analysis (CA) was used to detect general trends in the diet. CA is an eigenvalue technique that uses a matrix derived from a contingency table to obtain eigenvalues and eigenvectors, which become the principal axes (Davis 1986). The row and column coordinates are plotted, revealing possible niche relationships within the diet data (Graham and Vrijenhoek 1988). Using Minitab software (Minitab, Inc. 1998), CA was performed for size class and prey group to examine ontogenetic changes in diet. Percent IRI values for five prey categories (Teleostei, Crustacea, Elasmobranchii, Cephalopoda, and Unknown) were entered as columns and size class (≤ 60 cm PCL, 61-80 cm PCL, 81-100 cm PCL, and ≥ 100 cm PCL) as rows. CA was performed using %F values from the entire data set to verify these results.

The relationship of location to prey group was also examined by using CA on percent frequencies for the five aforementioned prey categories at five longline stations (W, V, T, M, and K; see Figure 3). There was an insufficient number of records for each station (21 or fewer) in the 2001-2002 data to use %IRI in the station analysis. CA was also done using %F data for the broader category of station type (Bay, Coastal, and Eastern Shore) and the five prey categories of

Figure 3: Map of five longline stations: W = Wreck Island, T = Triangle, V = Virginia Beach, M = Middleground, and K = Kiptopeke.



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Chesapeake Bay
Atlantic Ocean
W
K
M
T
V

Teleostei, Crustacea, Elasmobranchii, Cephalopoda, and Unknown. To examine the effect of time on diet composition, CA was performed using %F data for station type and decade against prey group for broad prey categories including the unknown category, as well as without the unknown category. In all cases, integer values of percentages were used.

Of particular interest is the diet of juvenile sandbar sharks and whether juvenile diet varies within and between regions of nursery ground. Prey group IRI data for juveniles (≤ 90 cm PCL) from Bay stations (n = 47 stomachs) and Eastern Shore stations (n = 143 stomachs) were examined using the chi-squared (χ^2) test. The prey groups used were Teleostei, Crustacea, and Other. Intraregional variation in diet was also examined using this test. Differences in frequencies of occurrence of crustaceans in stomachs of juvenile sandbar sharks (≤ 80 cm PCL) from three regions of the Eastern Shore (Wachapreague, Great Machipongo, and Sand Shoal Inlet) were evaluated using the chi-square test and CA. Crustaceans were pooled into four categories: mantis shrimp (*Squilla empusa*), portunid crab (blue crabs, lady crabs, and unidentified portunids), other (e.g., penaeid shrimp, mud shrimp, and spider crabs), and unidentified. Pooling the data into these categories resulted in fewer than 20% of the cells having values less than five, which is recommended for this procedure (Crow 1982; Cortés 1997). Significance was tested at the five-percent level. Correspondence analysis was performed using %F data from the entire data set for crustacean types in each of three Eastern Shore regions (Wachapreague, Machipongo, and Sand Shoal Inlet).

Multiple analysis of variance (MANOVA) was employed to further investigate trends identified in CA results. MANOVA has the advantage of looking at the correlation among multiple dependent variables in one procedure (Zar 1996). Because of the high number of subdivisions of the data necessary to run a MANOVA (station type, shark size, and prey type), which precluded the use of the more preferable weight or IRI indices, the analysis was run with frequency of occurrence ratios from the entire data set grouped by size class and station type. Before using MANOVA, the non-normally distributed frequency of occurrence data were transformed with the arcsine transformation, which is indicated for percentages or proportions. The arcsine, or inverse sine, transformation was performed using the equation $X' = \arcsin\sqrt{p}$, where X' is the transformed value and p is the observed proportion (Krebs 1989, Zar 1996). A two-way MANOVA was run in Minitab to compare the effects of station type and size class on prey type (dependent variables). Pillai's trace, which has been reported as a robust statistic that is good for general use, was used to test for significance (Zar 1996).

Larger sandbar sharks are known to eat other elasmobranchs, but the size at which this prey enters their diet remains unknown. Binary logistic regression analysis was used with presence/absence data to develop a relationship predicting the probability of elasmobranchs occurring in the stomach (Hosmer and Lemeshow 1989). Zeros were assigned to stomachs containing no elasmobranch remains, and ones were assigned to those stomachs with elasmobranch remains. Minitab software was used to perform the binary logistic regression of PCL versus presence/absence of elasmobranch. The probabilities ($\pi(x)$) were generated in Minitab using the following formula (Hosmer and Lemeshow 1989):

$$\pi(x) = (e^{b+ax})/(1 + e^{b+ax})$$

The values resulting from the use of the model were then transformed using the logit link function (Hosmer and Lemeshow 1989) to obtain the coefficients b and a:

$$g(x) = \ln\{\pi(x)/[1- \pi(x)]\} = b + ax$$

The statistic G, or the likelihood ratio of the model with and without the coefficients, was used to test the significance of the coefficients in the model. Its corresponding p-value was examined at the five percent significance level (Hosmer and Lemeshow 1989).

Bite radius measurements were plotted against PCL, and a non-linear regression was calculated. Because bite radius was only measured on a small number of sharks with stomach contents, values estimated using the regression equation were used for graphical comparison purposes.

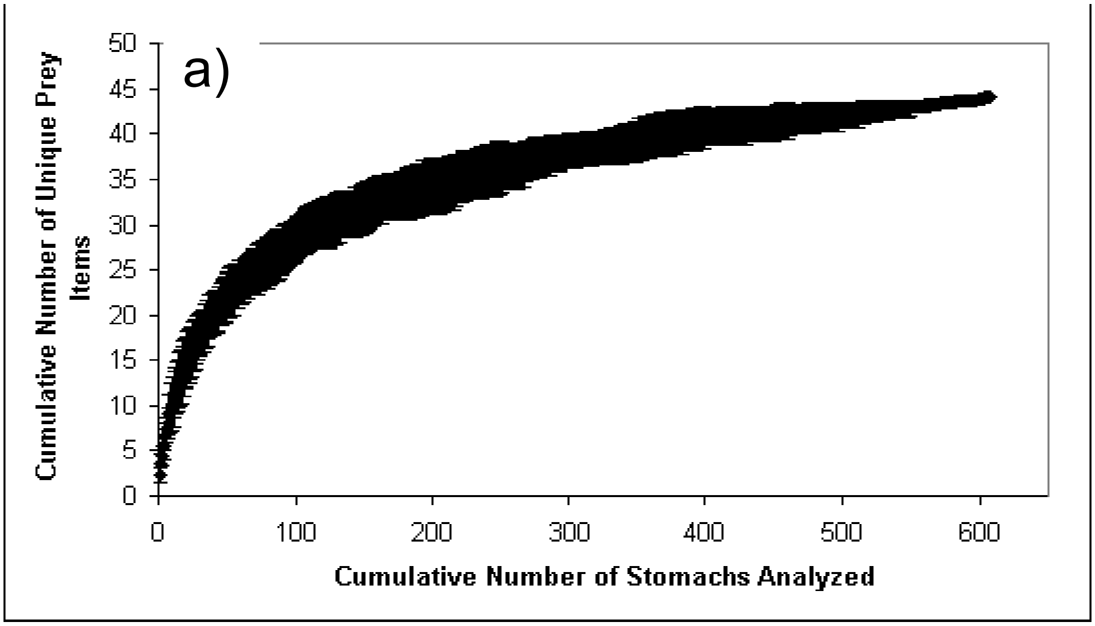
RESULTS

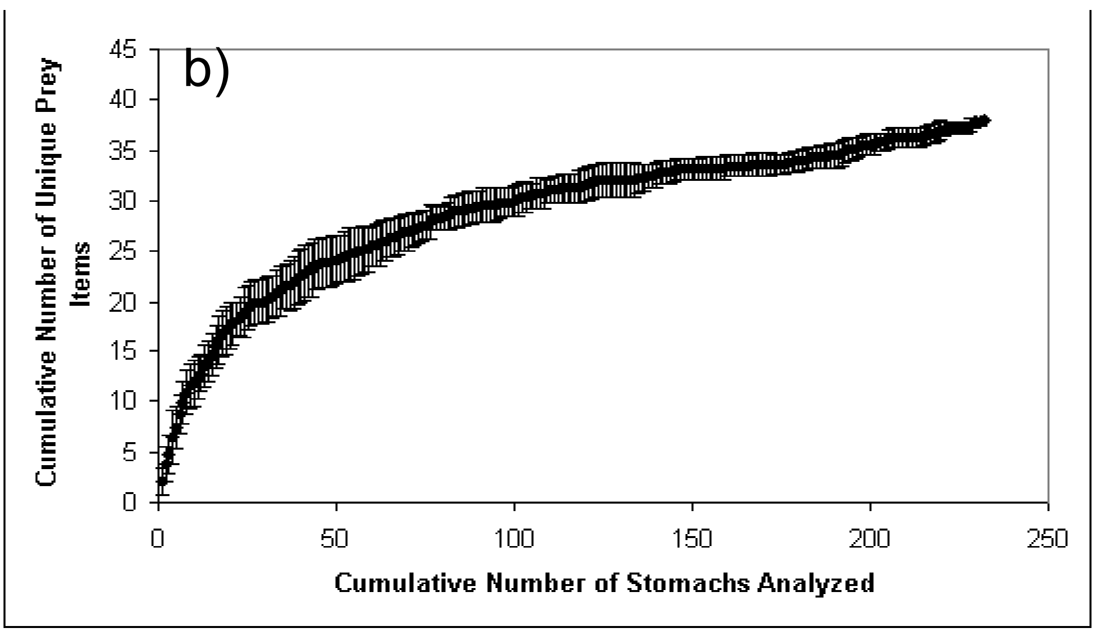
Stomach samples from 232 sandbar sharks measuring 40 to 150 cm PCL were collected from 2001 to 2002. Eighty-three of these samples were obtained with gillnets during 2002; the remaining 139 stomachs were obtained from animals caught on longline gear. Average PCL for the 2001-2002 samples was 69.3 cm (± 18.4 cm SD). VIMS Shark Ecology Program archival data yielded records of 376 sandbar sharks with stomachs containing food, ranging in size from 40 to 165 cm PCL with a mean PCL of 82.8 cm (± 27.3 cm SD). Of the total number of sharks caught in gillnets, 22 had empty stomachs (19%), whereas 83 had at least one food item (81%). Examination of the empty stomachs showed no indication of regurgitation. In the entire data set, the number of females in each size class was always greater than the number of males, and the female to male ratio increased drastically with increasing size. The smallest size class (≤ 60 cm PCL) consisted of 67 females and 65 males, but the largest size class (> 100 cm PCL) had 124 females and 8 males.

The cumulative prey curve for the entire data set of 2001-2002 samples and data sheet records (n = 608) appeared to approach an asymptote, indicating that sample size was adequate for this study (Figure 4a). The cumulative prey curve for the 2001-2002 data (n = 232) did not appear to approach an asymptote, but the rate of increase of prey items did slow after an initial rapid ascent (Figure 4b).

Figure 4a: Cumulative prey curve for all data, including archival records and 2001-2002 samples (n = 608).

Figure 4b: Cumulative prey curve for all 2001-2002 samples (n = 232).


a)
Cumulative Number of Unique Prey Items
Cumulative Number of Stomachs Analyzed
0
5
10
15
20
25
30
35
40
45
50
0
100
200
300
400
500
600


b)
Cumulative Number of Unique Prey Items
Cumulative Number of Stomachs Analyzed
0
5
10
15
20
25
30
35
40
45
0
50
100
150
200
250

Prey items from 28 families of bony fishes, 12 families of crustaceans, and 6 families of elasmobranchs were recorded or found in sandbar shark stomachs (Tables 1 and 2). Cephalopods, gastropods, bivalves, bryozoans, hydrozoans, plants, trash, and unidentified biological matter were also present (Table 3). In total, approximately 65 species were represented. (This number may be an underestimate if unidentified prey items represent previously uncounted species.) Of 608 shark stomachs reviewed in this study, two instances of cannibalism were recorded. A chunk of sandbar shark was found in the stomach of a 59 cm PCL female, and a whole sandbar shark pup was found in the stomach of a pregnant female (145 cm PCL). These samples were caught on a longline, so it is possible that the sandbar sharks were consumed as secondary baits. Prey items were consumed in chunks and whole. A few prey items consumed whole retained bite marks halfway along the body. In general, the carapaces of crustaceans found in *C. plumbeus* stomachs, particularly those of crabs, were soft in texture.

For the 2001-2002 samples (all sizes), males and females appeared to have similar diets with %IRI values of 58.1and 62.8 for teleosts. Importance of crustaceans was also similar at 37.8% for males and 32.6% for females. Schoener index of overlap values between the two groups were high, at 0.98 when using IRI and 0.89 when calculated using average wet weight.

Size Class

The smallest size class of sharks (≤ 60 cm PCL), or class I, consumed a variety of bony fishes, with unidentified fish occurring most frequently (Table 4).

Table 1: Scientific and common names of fish prey items found in sandbar shark stomachs with number of stomachs containing prey item.

Prey Item	Common Name	Number of Stomachs
Teleosts		
Anguillidae		
Anguilla rostrata	American eel	2
Congridae		
Conger oceanicus	conger eel	4
Unidentified eel		1
Clupeidae		
Alosa spp.	shad	2
Brevoortia spp.	menhaden	16
Brevoortia tyrannus	Atlantic menhaden	5
Etrumereus teres	round herring	4
Opisthonema oglinum	Atlantic thread herring	1
Unidentified clupeid		1
Engraulidae		
Anchoa hepsetus	striped anchovy	6
Anchoa mitchilli	bay anchovy	5
Anchoa spp.	anchovy	9
Unidentified engraulid		4
Cyprinodontidae		
Fundulus heteroclitus	mummichog	2
Fundulus majalis	striped killifish	1
Gadidae		
Urophycis regia	spotted hake	2
Urophycis spp.	hake	2
Unidentified gadiform		1
Lophiidae		
Lophius americanus	goosefish	2
Ophidiidae	cusk eels	1
Ammodytidae	sand lances	3
Carangidae	jacks	1
Ephippidae		
Chaetodipterus faber	Atlantic spadefish	1
Moronidae		
Morone saxatilis	striped bass	1
Mugilidae		
Mugil cephalus	striped mullet	1
Pomatomidae		
Pomatomus saltatrix	bluefish	9
Rachycentridae		
Rachycentron canadum	cobia	1
Sciaenidae		
Bairdiella chrysoura	silver perch	1
Cynoscion nebulosus	spotted seatrout	2
Cynoscion regalis	weakfish	12
Cynoscion spp.	seatrout	5
Leiostomus xanthurus	spot	9
Micropogonias undulatus	croaker	38
Unidentified sciaenid		10
Serranidae		
Centropristis striata	black sea bass	4

Prey Item	Common Name	Number of Stomachs
Sparidae		
Lagodon rhomboides	pinfish	1
Uranoscopidae		
Astroscopus guttatus	northern stargazer	7
Achiridae		
Trinectes maculatus	hogchoker	37
Cynoglossidae		
Symphurus plagiusa	black-cheeked tonguefish	3
Paralichthyidae		
Etropus microstomus	smallmouth flounder	3
Etropus spp.	smallmouth or fringed flounder	1
Paralichthys dentatus	summer flounder	3
Paralichthys spp.	left-eye flounder	1
Unidentified paralichthyid	parlichthyid flounders	1
Pleuronectidae		
Pleuronectes americanus	winter flounder	1
Scophthalmidae		
Scophthalmus aquosus	windowpane	4
Unidentified flatfish		14
Triglidae		
Prionotus carolinus	northern searobin	4
Prionotus spp.	searobin	6
Unidentified triglid		13
Fistularidae		
Fistularia tabacaria	bluespotted cornetfish	1
Syngnathidae	pipefishes/seahorses	1
Unidentified syngnathiform	pipefishes/coronetfishes	1
Tetradontidae		
Spheroides maculatus	northern puffer	1
Unidentified puffer		2
Unidentified teleost		191
Elasmobranchs		
Carcharhinidae		
Carcharhinus plumbeus	sandbar shark	2
Dasyatidae		
Dasyatis spp.	stingray	4
Myliobatidae	eagle rays	1
Rajidae		
Leucoraja erinacea	little skate	2
Raja eglanteria	clearnose skate	17
Rajid egg case	skate egg case	7
Unidentified rajid	skate	34
Rhinopteridae		
Rhinoptera bonasus	cownose ray	2
Triakidae		
Mustelus canis	smooth dogfish	1
Unidentified batoid	stingrays/skates	13
Unidentified shark	sharks	1
Unidentified elasmobranch	rays/skates/sharks	7

Table 2: Scientific and common names of crustacean prey items found in sandbar shark stomachs with number of stomachs containing prey item.

Prey Item	Common Name	Number of Stomachs
Squillidae		
Squilla empusa	mantis shrimp	108
Portunidae		
Arenaeus cribrarius	speckled crab	1
Callinectes sapidus	blue crab	45
Carcinus maenus	green crab	1
Ovalipes ocellatus	lady crab	37
Unidentified portunid	swimming crab	5
Majidae		
Libinia emarginata	common spider crab	7
Libinia spp.	spider crab	4
Pelia mutica	red-spotted spider crab	4
Unidentified majid	spider crabs	12
Cancridae		
Cancer irroratus	rock crab	2
Leucosiidae		
Persephona punctata	purse crab	1
Xanthidae	mud crabs	1
Unidentified crab		12
Paguridae		
Pagurus longicarpus	long-clawed hermit crab	1
Pagurus pollicaris	flat-clawed hermit crab	15
Pagurus spp.	hermit crab	6
Hippolytidae		
Hippolysmata wurdemanni	veined shrimp	1
Penaeidae		
Penaeus aztecus	brown shrimp	1
Penaeus duorarum	pink shrimp	1
Penaeus spp.	southern commercial shrimp	1
Callianassidae		
Calianassa atlantica	short-browed mud shrimp	1
Upogebiidae		
Upogebia affinus	flat-browed mud shrimp	21
Crangonidae		
Crangon septemspinosa	sand shrimp	2
Unidentified shrimp		1
Isopoda	isopod	1
Unidentified crustacean		11

Table 3: Scientific names and common names of mollusc, plant, and other prey items found in sandbar shark stomachs with number of stomachs containing prey item.

Prey Item	Common Name	Number of Stomachs
Molluscs		
Bivalves		
Ensis directus	razor clam	2
Mytilus spp.	mussel	2
Nucula proxima	near nut shell	1
Spissula solidissima	surf clam	1
Cephalopods		
Loligonidae		
Lolliguncula brevis	long-finned squid	7
Loligo pealei	long-finned squid	13
Unidentified loligonid	coastal squids	9
Ommastrephidae		
Illex spp.	boreal squid	1
Unidentified cephalopod		17
Gastropods		
Buccinidae	whelks	1
Littorina spp.	periwinkle	3
Nassarius obsoletus	mud dog whelk	1
Nassarius trivitattus	New England dog whelk	1
Nassarius spp.	dog whelk	4
Natacidae	moon shells	1
Nudibranchia	nudibranchs	2
Unidentified mollusc		1
Plants		
Aghardiella tenera	Agardh's red weed	1
Gracilaria sp.	red weed	2
Punctaria sp.	ribbon weed	1
Ulva sp.	sea lettuce	3
Zostera marina	eel grass	2
Unidentified plant		3
Other		
Anemone		1
Bryozoan		4
Hydrozoa		1
Limulus polyphemus	horseshoe crab	1
Polychaete		1
Trash		3
Tunicate		1
Unidentified invertebrate		1
Unidentified biological matter		47

Table 4: Prey item scientific and common names with frequency of occurrence values and percentages for 132 sandbar sharks less than 60 cm PCL.

Prey Item	Common Name	F	%F
Crustaceans			
Squillidae			
Squilla empusa	mantis shrimp	39	29.5
Portunidae			
Callinectes sapidus	blue crab	27	20.5
Ovalipes ocellatus	lady crab	7	5.3
Unidentified portunid	swimming crab	2	1.5
Majidae			
Libinia emarginata	common spider crab	3	2.3
Libinia spp.	spider crab	2	1.5
Pelia mutica	red-spotted spider crab	3	2.3
Unidentified majid	spider crabs	1	0.8
Cancridae			
Cancer irroratus	rock crab	1	0.8
Xanthidae	mud crabs	14	10.6
Unidentified crab		6	4.5
Paguridae			
Pagurus longicarpus	long-clawed hermit crab	1	0.8
Pagurus pollicaris	flat-clawed hermit crab	3	2.3
Pagurus spp.	hermit crab	2	1.5
Penaeidae			
Penaeus azteca	brown shrimp	1	0.8
Penaeus spp.	southern commercial shrimp	2	1.5
Callianassidae			
Callianassa atlantica	short-browed mud shrimp	1	0.8
Upogebiidae			
Upogebia affinus	flat-browed mud shrimp	1	0.8
Crangonidae			
Crangon septemspinosa	sand shrimp	1	0.8
Isopoda	isopod	1	0.8
Unidentified crustacean		5	3.8
Teleosts			
Anguillidae			
Anguilla rostrata	American eel	1	0.8
Clupeidae			
Alosa spp.	shad	1	0.8
Brevoortia spp.	menhaden	2	1.5
Brevoortia tyrannus	Atlantic menhaden	1	0.8
Unidentified clupeid		1	0.8
Engraulidae			
Anchoa hepsetus	striped anchovy	3	2.3
Anchoa mitchilli	bay anchovy	1	0.8
Anchoa spp.	anchovy	2	1.5
Cyprinodontidae			
Fundulus heteroclitus	mummichog	1	0.8
Gadidae			
Urophycis spp.	hake	1	0.8
Lophiidae			
Lophius americanus	goosefish	1	0.8
Mugilidae			
Mugil cephalus	striped mullet	1	0.8
Sciaenidae			

Prey Items	Common Name	F	%F
Cynoscion nebulosus	spotted seatrout	1	0.8
Cynoscion regalis	weakfish	3	2.3
Leiostomus xanthurus	spot	3	2.3
Micropogonias undulatus	croaker	6	4.5
Sparidae			
Lagodon rhomboides	pinfish	1	0.8
Achiridae			
Trinectes maculatus	hogchoker	7	5.3
Cynoglossidae			
Symphurus plagiusa	black-cheeked tonguefish	1	0.8
Parlichthyidae			
Etropus spp.	smallmouth or fringed flounder	1	0.8
Unidentified paralichthyid	left-eye flounder	1	0.8
Pleuronectidae			
Pleuronectes americanus	winter flounder	1	0.8
Scopthalmidae			
Scopthalmus aquosus	windowpane	2	1.5
Unidentified flatfish		2	1.5
Triglidae			
Prionotus carolinus	northern searobin	1	0.8
Prionotus spp.	searobin	3	2.3
Fistularidae			
Fistularia tabacaria	bluespotted cornetfish	1	0.8
Syngnathidae	pipefishes/seahorses	1	0.8
Unidentified syngnathiform	pipefishes/coronetfishes	1	0.8
Tetradontidae			
Spheroides maculatus	northern puffer	1	0.8
Unidentified teleost		35	26.5
Elasmobranchs			
Carcharhinidae			
Carcharhinus plumbeus	sandbar shark	1	0.8
Myliobatidae	eagle rays	1	0.8
Rhinopteridae			
Rhinoptera bonasus	cownose ray	1	0.8
Molluscs			
Bivalves		1	0.8
Mytilus spp.	mussel	1	0.8
Nucula proxima	near nut shell	1	0.8
Cephalopods			
Loligonidae			
Lolliguncula brevis	long-finned squid	4	3.0
Unidentified loligonid	coastal squids	1	0.8
Unidentified cephalopod		1	0.8
Gastropods			
Nassarius obsoletus	mud dog whelk	1	0.8
Nassarius spp.	dog whelk	2	1.5
Plants			
Punctaria sp.	ribbon weed	1	0.8
Ulva sp.	sea lettuce	1	0.8
Zostera marina	eel grass	1	0.8
Other			
Bryozoan		3	2.3
Hydrozoa		1	0.8
Trash		1	0.8
Tunicate		1	0.8
Unidentified biological matter		13	9.8

Hogchoker (*Trinectes maculatus*) and croaker (*Micropogonias undulatus*) were found in 5.3% and 4.5% of the stomachs, respectively. Of the crustaceans, the mantis shrimp, *Squilla empusa*, had the highest frequency of occurrence value at 29.5%, followed by blue crab (20.5%) and mud crabs (10.6%) (Table 4). In the subset of 2001-2002 samples, mantis shrimp, blue crab, and unidentified teleost had the largest IRI values at 43.0%, 36.5%, and 5.5%, respectively. Blue crab dominated by %W, but mantis shrimp occurred more frequently and in greater numbers. There did not appear to be any specialized predation on fishes, but crustaceans were targeted (Table 5; Figure 5). IRI values for broad prey categories (teleosts, crustaceans, elasmobranchs, cephalopods, unknown, and other) showed crustaceans dominating the diet at 67.6% followed by teleosts at 30.6%. The remaining categories all had %IRI values of less than one (Table 6). Cumulative prey curves for size class I from the entire data set and from the 2001-2002 subset of data, indicated that 132 and 89 stomachs adequately characterized most of the prey items, but rare ones may not have been accounted for (Figure 6a, b).

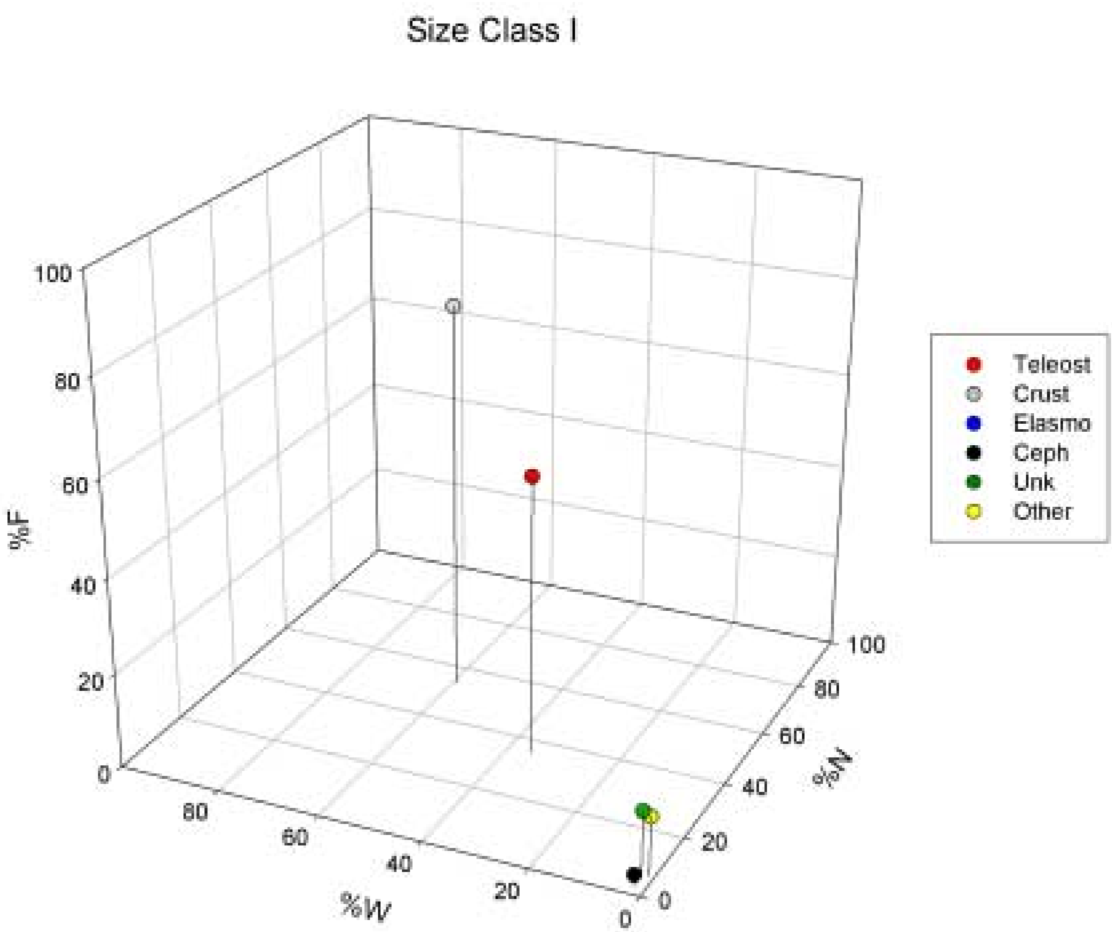
The diet of sharks in size class II (61-80 cm PCL) was more focused on teleosts. Unidentified teleosts were found in 37.1% of the stomachs examined. *Squilla empusa* also occurred relatively frequently (20.8%), but blue crab was only found in 5.1% of stomachs. Hogchoker and croaker were the most dominant of the identified fishes at 9.6% and 7.1%, respectively (Table 7). The 2001-2002 data indicated that mantis shrimp dominated the diet by frequency (44.2%), number (25.8%), weight (26.8%), and IRI (69.8%), followed by croaker at 14.4% IRI. The

Table 5: Prey item frequency (F), number (N), wet weight (W), and index of relative importance (IRI) values and percentages for 89 sandbar sharks ≤ 60 cm PCL.

Prey Item	No. Stom.	%F	No. Items	%N	Wet Wt. (g)	%W	IRI	%IRI
Crustaceans								
Squilla empusa	33	37.1	41	20.8	222.4	18.6	1460.2	43.0
Callinectes sapidus	24	27.0	29	14.7	375	31.3	1241.3	36.5
Ovalipes ocellatus	5	5.6	5	2.5	28.7	2.4	27.7	0.8
Unidentified portunid	2	2.2	2	1.0	6.4	0.5	3.5	0.1
Libinia emarginata	3	3.4	3	1.5	10.5	0.9	8.1	0.2
Libinia sp.	2	2.2	2	1.0	4	0.3	3.0	0.1
Pelia mutica	3	3.4	3	1.5	4.3	0.4	6.3	0.2
Upogebia affinus	14	15.7	15	7.6	26.8	2.2	155.0	4.6
Callianassa atlantica	1	1.1	1	0.5	0.4	0.0	0.6	0.0
Pagurus longicarpus	1	1.1	1	0.5	0.8	0.1	0.6	0.0
Pagurus pollicaris	2	2.2	2	1.0	1	0.1	2.5	0.1
Penaeus azteca	1	1.1	1	0.5	7.4	0.6	1.3	0.0
Penaeus spp.	2	2.2	2	1.0	5.2	0.4	3.3	0.1
Unidentified decapod	1	1.1	1	0.5	0	0.0	0.6	0.0
Unidentified crustacean	4	4.5	0	0.0	18.5	1.5	6.9	0.2
Teleosts								
Anguillidae								
Anguilla rostrata	1	1.1	1	0.5	15.2	1.3	2.0	0.1
Clupeidae								
Alosa spp.	1	1.1	2	1.0	11.9	1.0	2.3	0.1
Brevoortia tyrannus	1	1.1	1	0.5	2.7	0.2	0.8	0.0
Unidentified clupeid	1	1.1	1	0.5	1.7	0.1	0.7	0.0
Engraulidae								
Anchoa hepsetus	3	3.4	5	2.5	16.1	1.3	13.1	0.4
Anchoa mitchilli	1	1.1	2	1.0	7.9	0.7	1.9	0.1
Anchoa spp.	2	2.2	2	1.0	1	0.1	2.5	0.1
Cyprinodontidae								
Fundulus heteroclitus	1	1.1	1	0.5	0.1	0.0	0.6	0.0
Lophiidae								
Lophius americanus	1	1.1	1	0.5	2.1	0.2	1.0	0.0
Achiridae								
Trinectes maculatus	7	7.9	8	4.1	103.4	8.6	99.8	2.9
Cynoglossidae								
Symphurus plagiusa	1	1.1	1	0.5	2.6	0.2	0.8	0.0
Paralichthyidae	1	1.1	1	0.5	17.4	1.5	2.2	0.1
Pleuronectidae								
Pleuronectes americanus	1	1.1	2	1.0	8.3	0.7	1.9	0.1
Scopthalmidae								
Scopthalmus aquosus	2	2.2	2	1.0	8.7	0.7	3.9	0.1
Muglidae								
Mugil cephalus	1	1.1	1	0.5	19.7	1.6	2.4	0.1
Sciaenidae								
Cynoscion nebulosus	1	1.1	1	0.5	0.1	0.0	0.6	0.0
Cynoscion regalis	3	3.4	3	1.5	18.6	1.6	10.4	0.3
Leiostomus xanthurus	2	2.2	2	1.0	41.6	3.5	10.1	0.3

Prey Item	No. Stom.	%F	No. Items	%N	Wet Wt. (g)	%W	IRI	%IRI
Micropogonias undulatus	6	6.7	6	3.0	20.7	1.7	32.2	0.9
Sparidae								
Lagodon rhomboides	1	1.1	1	0.5	0	0.0	0.6	0.0
Syngnathiformes	1	1.1	1	0.5	0.2	0.0	0.6	0.0
Fistulariidae								
Fistularia tabacaria	1	1.1	1	0.5	2.1	0.2	0.8	0.0
Tetradontidae								
Spheroides maculatus	1	1.1	1	0.5	56.1	4.7	5.8	0.2
Triglidae								
Prionotus carolinus	1	1.1	1	0.5	7	0.6	1.2	0.0
Prionotus spp.	3	3.4	4	2.0	25.6	2.1	14.0	0.4
Unidentified teleost	15	16.9	16	8.1	36.1	3.0	187.7	5.5
Bivalves								
Mytilus spp.	1	1.1	1	0.5	1.6	0.1	0.7	0.0
Unidentified bivalve	1	1.1	1	0.5	0.2	0.0	0.6	0.0
Cephalopods								
Loligonidae	1	1.1	1	0.5	0.1	0.0	0.6	0.0
Lolliguncula brevis	4	4.5	4	2.0	23.6	2.0	18.0	0.5
Gastropods								
Ilyanassa obsoleta	1	1.1	1	0.5	0.4	0.0	0.6	0.0
Nassaria spp.	2	2.2	2	1.0	1.2	0.1	2.5	0.1
Nucula proxima	1	1.1	1	0.5	0.1	0.0	0.6	0.0
Plants								
Zostera marina	1	1.1	1	0.5	1.5	0.1	0.7	0.0
Punctaria sp.	1	1.1	1	0.5	0.1	0.0	0.6	0.0
Ulva sp.	1	1.1	1	0.5	2.7	0.2	0.8	0.0
Other								
Bryozoan	2	2.2	2	1.0	0.2	0.0	2.3	0.1
Hydroid	1	1.1	1	0.5	0.6	0.1	0.6	0.0
Tunicate	1	1.1	1	0.5	1.7	0.1	0.7	0.0
Unidentified biological matter	12	13.5	3	1.5	25.4	2.1	49.1	1.4

Figure 5: Number (%N), weight (%W), and frequency (%F) indices for size class I (≤ 60 cm PCL) from 2001-2002 data (n = 89).



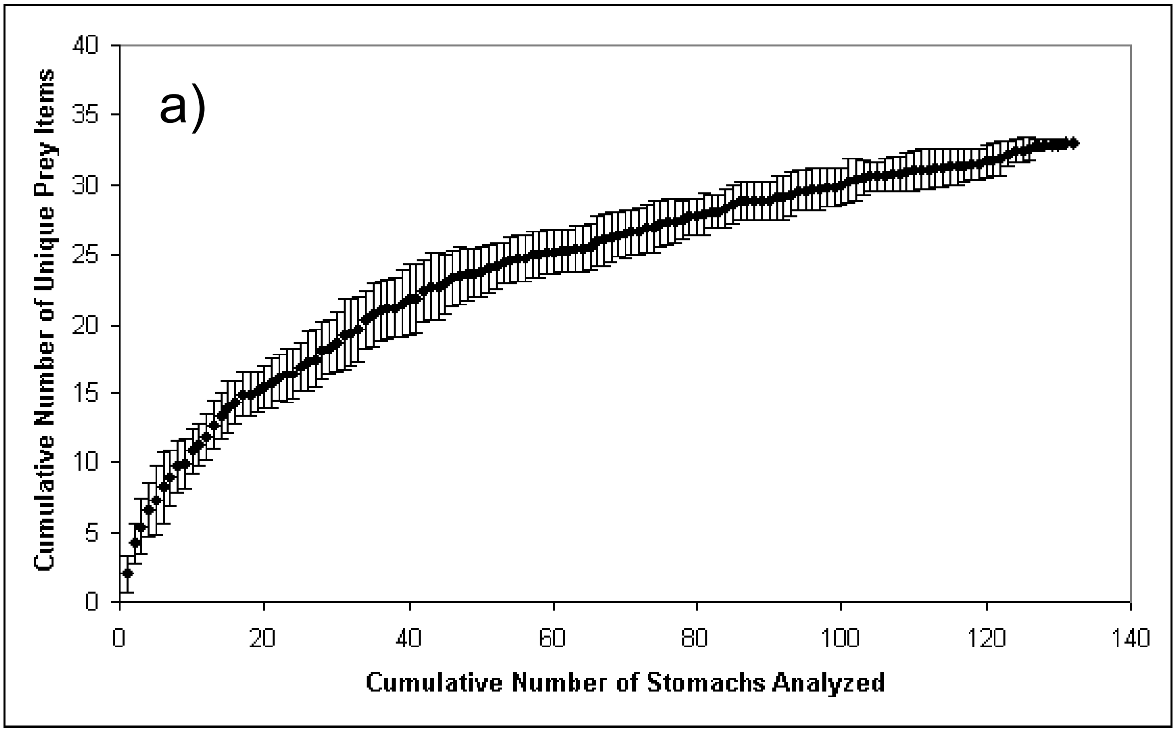
Size Class I
%F
%W
%N
100
80
60
40
20
0
Teleost
Crust
Elasmo
Ceph
Unk
Other

Table 6: Frequency of occurrence, number, weight, and index of relative importance (IRI) values for prey categories by size class. Sample sizes are 89, 77, 58, and 8 for classes I, II, III, and IV, respectively.

	n	%F	n	%N	n (g)	%W	IRI	%IRI
Size Class I (≤ 60 cm PCL)								
Teleost	52.0	58.4	71.0	35.5	428.0	35.6	4157.0	30.6
Crustacean	72.0	80.9	108.0	54.0	713.2	59.4	9174.2	67.6
Elasmobranch	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cephalopod	5.0	5.6	5.0	2.5	23.7	2.0	25.1	0.2
Unknown	12.0	13.5	12.0	6.0	25.4	2.1	109.4	0.8
Other	11.0	12.4	13.0	6.5	10.3	0.9	90.9	0.7
Size Class II (61-80 cm PCL)								
Teleost	48.0	62.3	80.0	44.0	799.1	53.0	6042.6	54.0
Crustacean	50.0	64.9	76.0	41.8	467.4	31.0	4723.7	42.2
Elasmobranch	9.0	11.7	9.0	4.9	204.1	13.5	216.0	1.9
Cephalopod	4.0	5.2	7.0	3.8	9.9	0.7	23.4	0.2
Unknown	11.0	14.3	11.0	6.0	12.4	0.8	98.1	0.9
Other	7.0	9.1	9.0	4.9	15.5	1.0	54.3	0.5
Size Class III (81-100 cm PCL)								
Teleost	37.0	63.8	60.0	36.8	1960.7	52.2	5681.1	55.1
Crustacean	37.0	63.8	65.0	39.9	492.0	13.1	3380.2	32.8
Elasmobranch	11.0	19.0	15.0	9.2	1200.0	32.0	781.0	7.6
Cephalopod	9.0	15.5	16.0	9.8	48.4	1.3	172.3	1.7
Unknown	16.0	27.6	16.0	9.8	25.0	0.7	289.2	2.8
Other	2.0	3.4	2.0	1.2	26.8	0.7	6.7	0.1
Size Class IV (> 100 cm PCL)								
Teleost	4.0	50.0	6.0	42.9	254.3	50.8	4684.8	51.2
Crustacean	4.0	50.0	4.0	28.6	23.8	4.8	1666.5	18.2
Elasmobranch	3.0	37.5	3.0	21.4	214.7	42.9	2413.2	26.3
Cephalopod	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unknown	2.0	25.0	2.0	14.3	7.4	1.5	394.1	4.3
Other	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Figure 6a: Cumulative prey curve for size class I (≤ 60 cm PCL) from all data, including archival records and 2001-2002 data (n = 132).

Figure 6b: Cumulative prey curve for size class I (≤ 60 cm PCL) from 2001-2002 data (n = 89).


a)
Cumulative Number of Unique Prey Items
Cumulative Number of Stomachs Analyzed
0
5
10
15
20
25
30
35
40
0
20
40
60
80
100
120
140

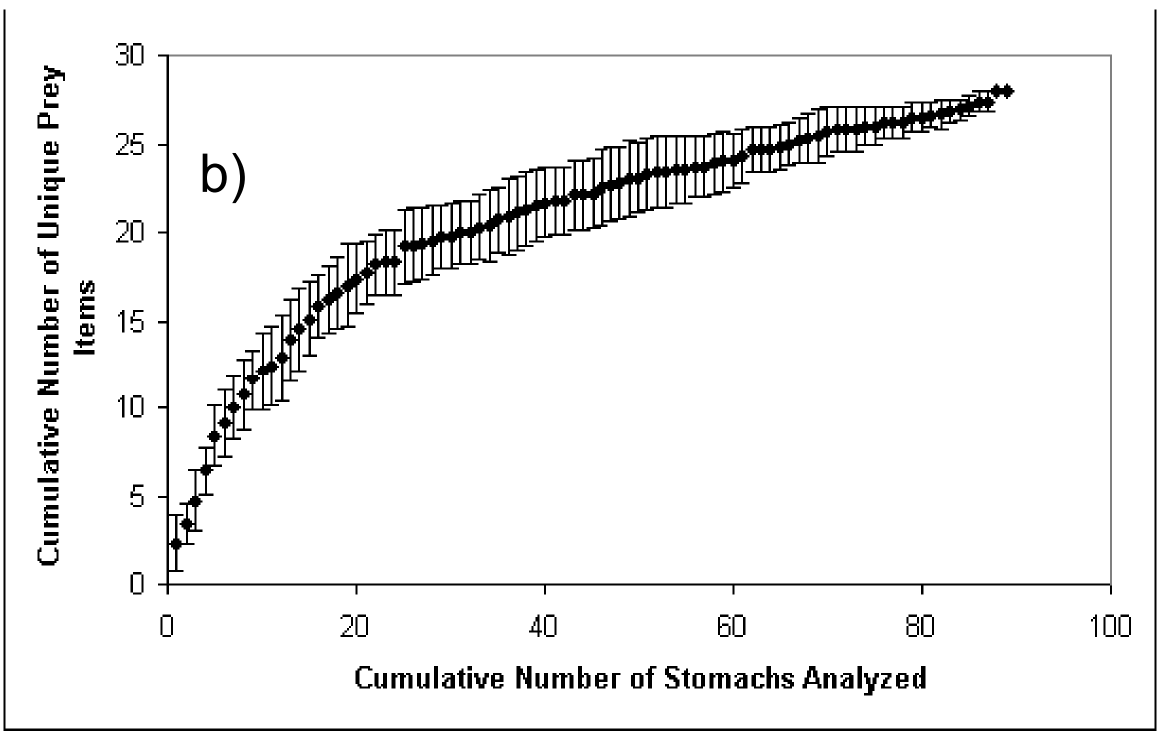

b)
Cumulative Number of Unique Prey Items
Cumulative Number of Stomachs Analyzed
0
5
10
15
20
25
30
0
20
40
60
80
100

Table 7: Prey item scientific and common names with frequency of occurrence (F) values and percentages for 197 sandbar sharks between 61 and 80 cm PCL.

Prey Item	Common Name	F	%F
Crustaceans			
Squillidae			
Squilla empusa	mantis shrimp	41	20.8
Portunidae			
Arenaeus cribrarius	speckled crab	1	0.5
Callinectes sapidus	blue crab	10	5.1
Ovalipes ocellatus	lady crab	7	3.6
Majidae			
Libinia emarginata	common spider crab	3	1.5
Libinia spp.	spider crab	1	0.5
Unidentified majid	spider crabs	2	1.0
Unidentified crab		3	1.5
Paguridae			
Pagurus pollicaris	flat-clawed hermit crab	8	4.1
Pagurus spp.	hermit crab	2	1.0
Penaeidae			
Penaeus duorarum	pink shrimp	1	0.5
Upogebiidae			
Upogebia affinus	flat-browed mud shrimp	5	2.5
Crangonidae			
Crangon septemspinosa	sand shrimp	1	0.5
Unidentified shrimp		1	0.5
Unidentified crustacean		4	2.0
Teleosts			
Congridae			
Conger oceanicus	conger eel	2	1.0
Clupeidae			
Alosa spp.	shad	1	0.5
Brevoortia spp.	menhaden	6	3.0
Brevoortia tyrannus	Atlantic menhaden	1	0.5
Etrumereus teres	round herring	2	1.0
Opisthonema oglinum	Atlantic thread herring	1	0.5
Engraulidae			
Anchoa hepsetus	striped anchovy	2	1.0
Anchoa mitchilli	bay anchovy	1	0.5
Anchoa spp.	anchovy	5	2.5
Unidentified engraulid		2	1.0
Cyprinodontidae			
Fundulus heteroclitus	mummichog	1	0.5
Fundulus majalis	striped killifish	1	0.5
Gadidae			
Urophycis regia	spotted hake	1	0.5
Ophidiidae	cusk eels	1	0.5
Ephippidae			
Chaetodipterus faber	Atlantic spadefish	1	0.5
Pomatomidae			
Pomatomus saltatrix	bluefish	1	0.5
Sciaenidae			
Cynoscion regalis	weakfish	4	2.0
Cynoscion spp.	seatrout	3	1.5
Leiostomus xanthurus	spot	3	1.5
Micropogonias undulatus	croaker	14	7.1

Prey Item	Common Name	F	%F
Unidentified sciaenid	drums	6	3.0
Serranidae			
Centropristis striata	black sea bass	1	0.5
Sparidae			
Stenotomus chrysops	scup	3	1.5
Achiridae			
Trinectes maculatus	hogchoker	19	9.6
Cynoglossidae			
Symphurus plagiusa	black-cheeked tonguefish	2	1.0
Paralichthyidae			
Paralichthys spp.	left-eye flounder	1	0.5
Scophthalmidae			
Scophthalmus aquosus	windowpane	2	1.0
Unidentified flatfish		5	2.5
Triglidae			
Prionotus carolinus	northern searobin	1	0.5
Prionotus spp.	searobin	3	1.5
Unidentified triglid		1	0.5
Tetradontidae	puffers	2	1.0
Unidentified teleost		73	37.1
Elasmobranchs			
Dasyatidae			
Dasyatis spp.	stingray	1	0.5
Rajidae			
Raja eglanteria	clearnose skate	4	2.0
Unidentified rajid	skate	10	5.1
Unidentified batoid	stingrays/skates	2	1.0
Unidentified elasmobranch	rays/skates/sharks	3	1.5
Molluscs			
Cephalopods			
Loligonidae			
Lolliguncula brevis	brief squid	2	1.0
Unidentified loligonid	coastal squids	2	1.0
Ommastrephidae			
Illex spp.	boreal squid	1	0.5
Unidentified cephalopod		4	2.0
Gastropods			
Buccinidae	whelks	1	0.5
Littorina spp.	periwinkle	1	0.5
Natacidae	moon shells	1	0.5
Nassarius trivitattus	New England dog whelk	1	0.5
Plants			
Gracilaria sp.	red weed	2	1.0
Ulva sp.	sea lettuce	2	1.0
Zostera marina	eel grass	1	0.5
Unidentified plant		3	1.5
Other			
Anemone		1	0.5
Bryozoan		1	0.5
Trash		1	0.5
Unidentified invertebrate		1	0.5
Unidentified biological matter		15	7.6

remaining prey items had %IRI values of less than 5% (Table 8). From a broader perspective, bony fishes dominated the diet at 54.0% IRI, followed by crustaceans at 42.2% IRI. The remaining categories—elasmobranchs, cephalopods, unknown, and other—had %IRI values of less than five (Table 6). Bony fishes and crustaceans had similar %F and %N values, but fishes had higher %W (Figure 7). The rapid then gradual increase in slope of the cumulative prey curves for the two datasets (complete and 2001-2002) indicate that most of the diet of this size class is represented; some prey items may not be included, but the majority has been accounted for by the 197 and 77 stomachs (Figures 8a, b).

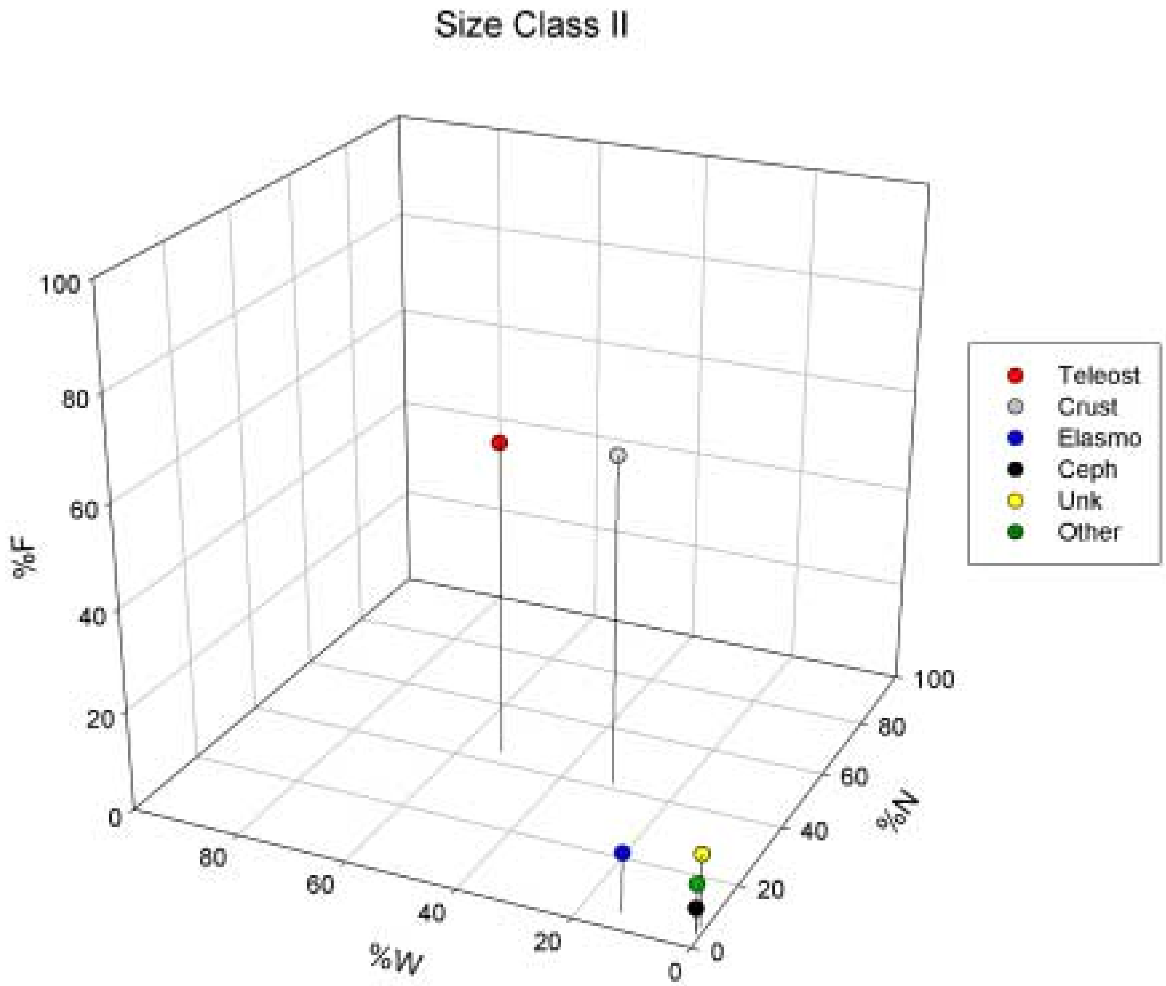
Size class III (81-100 cm PCL) shark stomachs in the 2001-2002 data subset had a predominance of bony fishes (%IRI = 55.1), as well as a substantial proportion of crustaceans (%IRI = 32.8). Elasmobranchs were also important at 7.6% IRI (Table 6), and by weight were more important than crustaceans. Bony fishes and crustaceans had similar %N and %F values, but fishes were more important by weight (Figure 9). In size class III stomachs from the entire data set, unidentified teleosts occurred most often (28.6%), followed by mantis shrimp (15.6%), lady crab (*Ovalipes ocellatus*, 11.6%), and croaker (9.5%) (Table 9). From the 2001-2002 subset of data, mantis shrimp had the highest %F and %N, but croaker and clearnose skate (*Raja eglanteria*) dominated by weight. Mantis shrimp, croaker, and unidentified teleost had the highest %IRI values (35.6%, 22.4%, and 11.8%, respectively) (Table 10). The cumulative prey curve for the

Table 8: Prey item frequency (F), number (N), wet weight (W), and index of relative importance (IRI) values and percentages for 77 sandbar sharks between 61 and 80 cm PCL.

Prey Item	No. Stom.	%F	No. Items	%N	Wet Wt. (g)	%W	IRI	%IRI
Crustaceans								
Squilla empusa	34	44.2	47	25.8	401.5	26.8	2325.4	69.8
Callinectes sapidus	4	5.2	4	2.2	9.4	0.6	14.7	0.4
Ovalipes ocellatus	2	2.6	2	1.1	1.1	0.1	3.0	0.1
Arenaeus cribrarius	1	1.3	1	0.5	0.9	0.1	0.8	0.0
Libinia emarginata	3	3.9	3	1.6	6.1	0.4	8.0	0.2
Libinia spp.	1	1.3	1	0.5	7.7	0.5	1.4	0.0
Upogebia affinus	5	6.5	6	3.3	12.7	0.8	26.9	0.8
Pagurus pollicaris	6	7.8	7	3.8	22	1.5	41.4	1.2
Penaeus duorarum	1	1.3	1	0.5	4.1	0.3	1.1	0.0
Unidentified shrimp	1	1.3	1	0.5	0.1	0.0	0.7	0.0
Unidentified crustacean	3	3.9	3	1.6	1.8	0.1	6.9	0.2
Teleosts								
Congridae								
Conger oceanicus	2	2.6	2	1.1	58.6	3.9	13.0	0.4
Clupeidae								
Alosa spp.	1	1.3	1	0.5	37.2	2.5	14.9	0.4
Brevoortia tyrannus	1	1.3	1	0.5	96.5	6.5	9.1	0.3
Etrumereus teres	2	2.6	3	1.6	23.9	1.6	8.4	0.3
Engraulidae								
Anchoa hepsetus	2	2.6	3	1.6	7.9	0.5	5.7	0.2
Anchoa mitchilli	1	1.3	1	0.5	2.8	0.2	1.0	0.0
Anchoa spp.	5	6.5	8	4.4	2.1	0.1	29.5	0.9
Cyprinodontidae								
Fundulus heteroclitus	1	1.3	1	0.5	4	0.3	1.1	0.0
Fundulus majalis	1	1.3	1	0.5	3.3	0.2	1.0	0.0
Gadidae								
Urophycis regia	1	1.3	1	0.5	0	0.0	0.7	0.0
Achiridae								
Trinectes maculatus	7	9.1	8	4.4	87.8	5.9	93.3	2.8
Cynoglossidae								
Symphurus plagiusa	2	2.6	4	2.2	9.1	0.6	7.3	0.2
Paralichthyidae								
Paralichthys spp.	1	1.3	1	0.5	0.5	0.0	0.8	0.0
Unidentified flatfish	2	2.6	2	1.1	2.1	0.1	3.2	0.1
Scophthalmidae								
Scophthalmus aquosus	1	1.3	1	0.5	9.8	0.7	1.6	0.0
Ephippidae								
Chaetodipterus faber	1	1.3	1	0.5	14.2	0.9	1.9	0.1
Sciaenidae								
Cynoscion regalis	3	3.9	4	2.2	120.2	8.0	39.9	1.2
Cynoscion spp.	2	2.6	2	1.1	16.2	1.1	5.7	0.2
Micropogonias undulatus	13	16.9	19	10.4	268.3	17.9	479.0	14.4
Unidentified sciaenid	1	1.3	1	0.5	1.8	0.1	0.9	0.0

Prey Item	No. Stom.	%F	No. Items	%N	Wet Wt. (g)	%W	IRI	%IRI
Sparidae								
Stenotomus chrysops	1	1.3	1	0.5	0.3	0.0	0.7	0.0
Triglidae								
Prionotus carolinus	1	1.3	1	0.5	10.4	0.7	1.6	0.0
Prionotus spp.	3	3.9	3	1.6	5.8	0.4	7.9	0.2
Unidentified teleost	9	11.7	10	5.5	16.3	1.1	77.0	2.3
Elasmobranchs								
Rajidae								
Raja eglanteria	3	3.9	3	1.6	38.3	2.6	16.4	0.5
Unidentified rajid	4	5.2	4	2.2	65.6	4.4	34.2	1.0
Unidentified elasmobranch	2	2.6	2	1.1	100.2	6.7	20.3	0.6
Cephalopods								
Loligonidae	2	2.6	5	2.7	3.7	0.2	7.8	0.2
Lolliguncula brevis	2	2.6	2	1.1	6.2	0.4	3.9	0.1
Gastropods								
Nassarius trivitattus	1	1.3	2	1.1	0.2	0.0	1.4	0.0
Plants								
Gracilaria sp.	2	2.6	2	1.1	13	0.9	5.1	0.2
Ulva sp.	2	2.6	2	1.1	1.2	0.1	3.1	0.1
Unidentified algae	2	2.6	2	1.1	1	0.1	3.0	0.1
Other								
Bryozoan	1	1.3	1	0.5	0.1	0.0	0.7	0.0
Unidentified biological matter	1	1.3	1	0.5	0.0	0.0	0.7	0.0

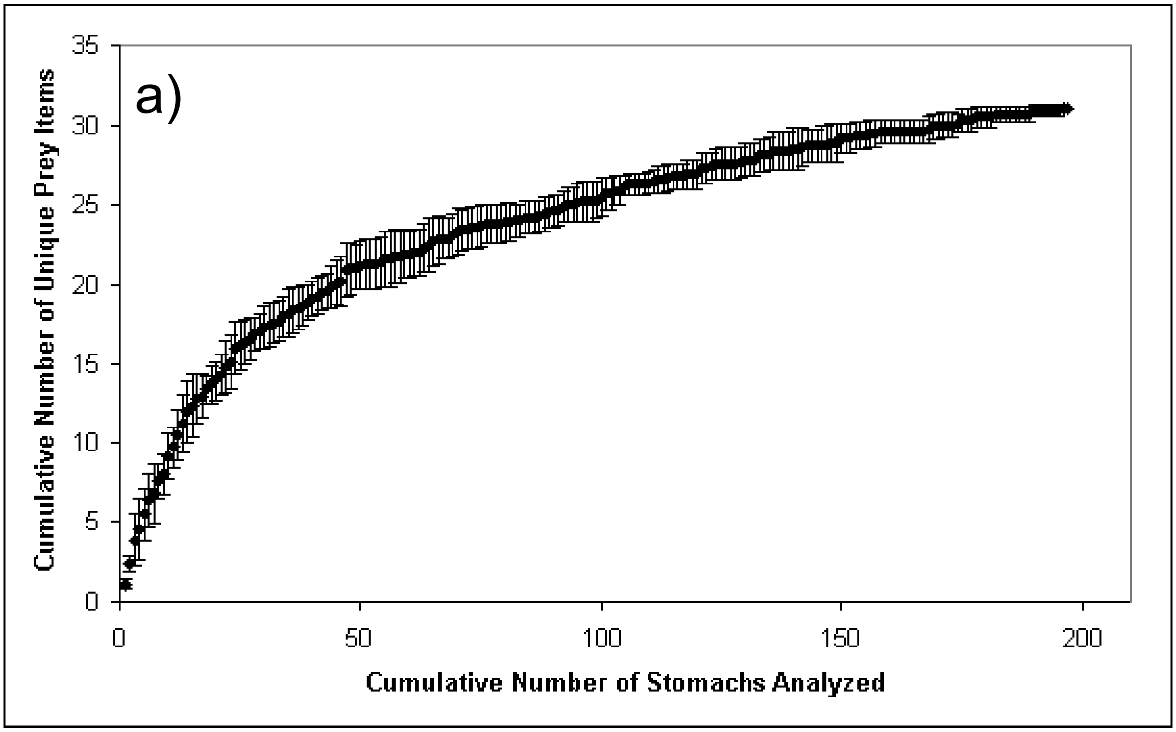
Figure 7: Number (%N), weight (%W), and frequency (%F) indices for size class II (61-80 cm PCL) from 2001-2002 samples (n = 77).



Size Class II
%F
100
80
60
40
20
0
%W
80
60
40
20
0
%N
100
80
60
40
20
0
Teleost
Crust
Elasmo
Ceph
Unk
Other

Figure 8a: Cumulative prey curve for size class II (61-80 cm PCL), including archival records and 2001-2002 samples (n = 197).

Figure 8b: Cumulative prey curve for size class II (61-80 cm PCL) from 2001-2002 samples (n = 77).


a)
Cumulative Number of Unique Prey Items
Cumulative Number of Stomachs Analyzed
0
5
10
15
20
25
30
35
0
50
100
150
200

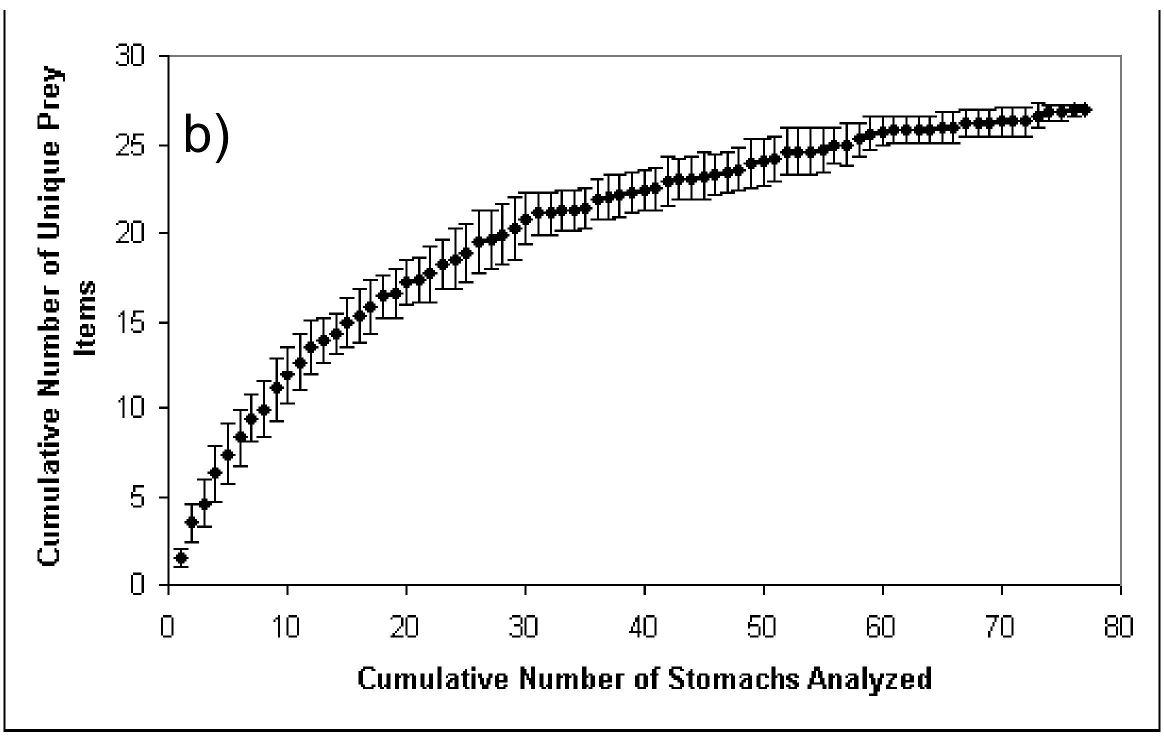

b)
Cumulative Number of Unique Prey Items
Cumulative Number of Stomachs Analyzed
0
5
10
15
20
25
30
0
10
20
30
40
50
60
70
80

Figure 9: Number (%N), weight (%W), and frequency (%F) indices for size class III (81-100 cm PCL) sandbar sharks from 2001-2002 samples (n = 58).

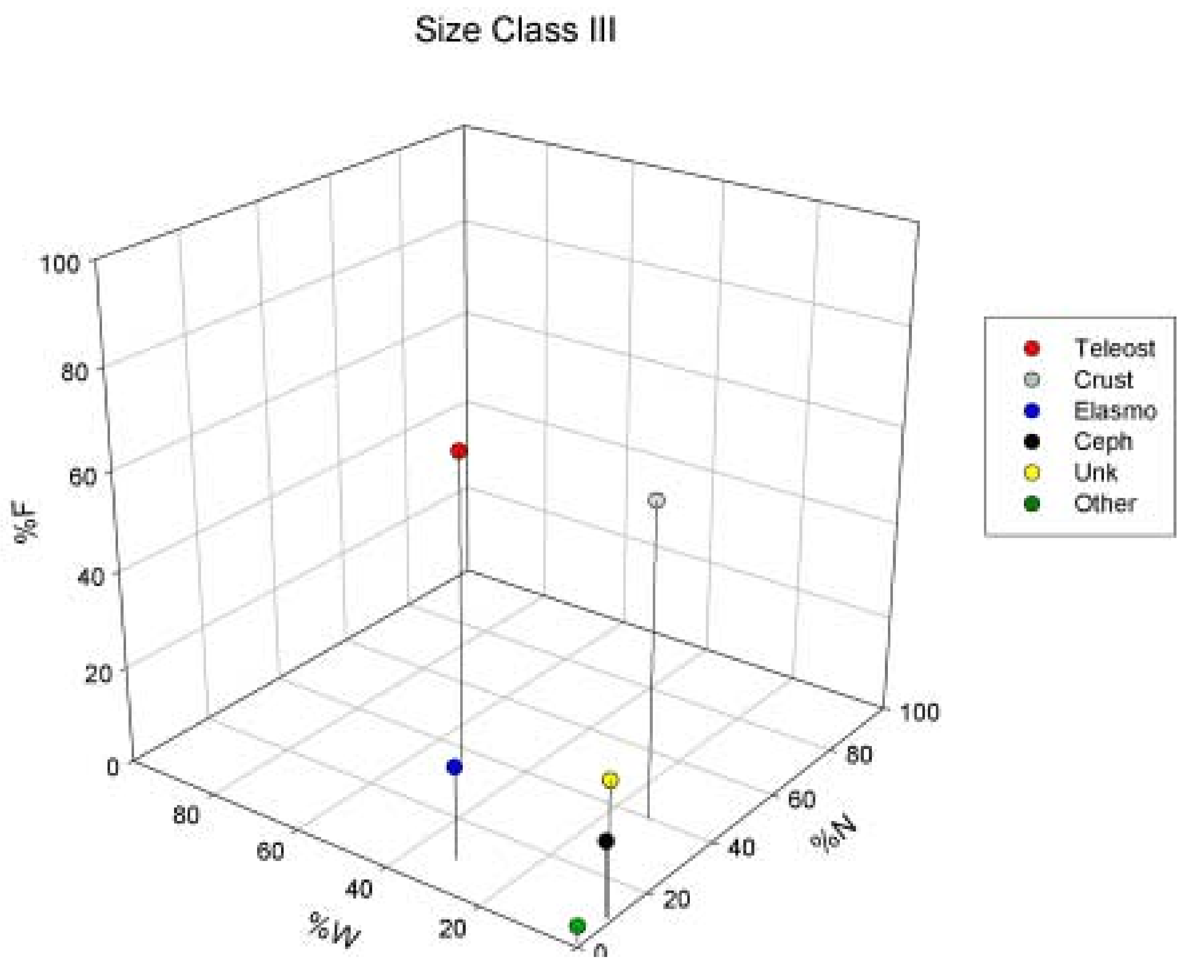

Size Class III
%F
100
80
60
40
20
0
%W
80
60
40
20
%N
0
20
40
60
80
100
Teleost
Crust
Elasmo
Ceph
Unk
Other

Table 9: Prey item scientific and common names with frequency of occurrence (F) values and percentages for 147 sandbar sharks between 81 and 100 cm PCL.

Prey Item	Common Name	F	%F
Crustaceans			
Squillidae			
Squilla empusa	mantis shrimp	23	15.6
Portunidae			
Callinectes sapidus	blue crab	7	4.8
Ovalipes ocellatus	lady crab	17	11.6
Unidentified portunid	swimming crab	1	0.7
Majidae			
Libinia emarginata	common spider crab	1	0.7
Libinia spp.	spider crab	1	0.7
Pelia mutica	red-spotted spider crab	1	0.7
Unidentified majid	spider crabs	4	2.7
Cancridae			
Cancer irroratus	rock crab	1	0.7
Leucosiidae			
Persephona punctata	purse crab	1	0.7
Unidentified crab		1	0.7
Paguridae			
Pagurus pollicaris	flat-clawed hermit crab	4	2.7
Pagurus spp.	hermit crab	1	0.7
Hippolytidae			
Hippolysmata wurdemanni	veined shrimp	1	0.7
Penaeidae			
Unidentified penaeid	southern commercial shrimps	1	0.7
Upogebiidae			
Upogebia affinus	flat-browed mud shrimp	2	1.4
Unidentified crustacean		2	1.4
Teleosts			
Congridae			
Conger oceanicus	conger eel	1	0.7
Unidentified eel		1	0.7
Clupeidae			
Brevoortia spp.	menhaden	6	4.1
Brevoortia tyrannus	Atlantic menhaden	3	2.0
Etrumeus teres	round herring	2	1.4
Engraulidae			
Anchoa hepsetus	striped anchovy	1	0.7
Anchoa mitchilli	bay anchovy	3	2.0
Anchoa spp.	anchovy	2	1.4
Unidentified engraulid		1	0.7
Gadidae			
Urophycis regia	spotted hake	1	0.7
Unidentified gadiform		1	0.7
Lophiidae			
Lophius americanus	goosefish	1	0.7
Ammodytidae	sand lances	1	0.7
Carangidae	jacks	1	0.7
Moronidae			
Morone saxatilis	striped bass	1	0.7

Prey Items	Common Name	F	%F
Sciaenidae			
Cynoscion nebulosus	spotted seatrout	1	0.7
Cynoscion regalis	weakfish	5	3.4
Cynoscion spp.	seatrout	2	1.4
Leiostomus xanthurus	spot	2	1.4
Micropogonias undulatus	croaker	14	9.5
Unidentified sciaenid	drums	2	1.4
Serranidae			
Centropristis striata	black sea bass	1	0.7
Uranoscopidae			
Astroscopus guttatus	northern stargazer	2	1.4
Achiridae			
Trinectes maculatus	hogchoker	10	6.8
Paralichthyidae			
Etropus microstomus	smallmouth flounder	3	2.0
Paralichthys dentatus	summer flounder	3	2.0
Unidentified flatfish		6	4.1
Triglidae	searobins	1	0.7
Unidentified teleost		42	28.6
Elasmobranchs			
Rajidae			
Raja eglanteria	clearnose skate	8	5.4
Rajid egg case	skate egg case	5	3.4
Unidentified rajid	skate	7	4.8
Unidentified batoid	skates/stingrays	5	3.4
Unidentified elasmobranch	skates/stingrays/sharks	1	0.7
Unidentified shark		1	0.7
Molluscs			
Bivalves			
Ensis directus	razor clam	1	0.7
Spissula solidissima	surf clam	1	0.7
Cephalopods			
Loligonidae			
Lolliguncula brevis	brief squid	1	0.7
Loligo pealei	long-finned squid	5	3.4
Unidentified loligonid	coastal squids	6	4.1
Unidentified cephalopod		2	1.4
Gastropods			
Nassariidae	dog whelks	1	0.7
Plants			
Aghardiella tenera	Agardh's red weed	1	0.7
Other			
Trash		1	0.7
Unidentified biological matter		16	10.9

Table 10: Prey item frequency (F), number (N), wet weight (W), and index of relative importance (IRI) values and percentages for 58 sandbar sharks between 81 and 100 cm PCL.

Prey Item	No. Stom.	%F	No. Items	%N	Wet Wt. (g)	%W	IRI	%IRI
Crustaceans								
Squilla empusa	19	32.8	33	20.2	342.6	9.2	963.1	35.6
Callinectes sapidus	4	6.9	4	2.5	14.2	0.4	19.5	0.7
Ovalipes ocellatus	9	15.5	15	9.2	63.5	1.7	169.1	6.3
Libinia emarginata	1	1.7	1	0.6	4.3	0.1	1.3	0.0
Libinia spp.	1	1.7	1	0.6	5.2	0.1	1.3	0.0
Pelia mutica	1	1.7	1	0.6	0.5	0.0	1.1	0.0
Persephona punctata	1	1.7	1	0.6	0.8	0.0	1.1	0.0
Upogebia affinus	2	3.4	2	1.2	5.6	0.1	4.7	0.2
Pagurus pollicaris	4	6.9	5	3.1	49.8	1.3	30.3	1.1
Hippolysmata wurdemanni	1	1.7	1	0.6	0.9	0.0	1.1	0.0
Unidentified crustacean	2	3.4	1	0.6	1.9	0.1	2.3	0.1
Teleosts								
Anguilliformes	1	1.7	1	0.6	8.4	0.2	1.4	0.1
Clupeidae								
Brevoortia tyrannus	3	5.2	3	1.8	97.4	2.6	23.0	0.8
Etrumereus teres	2	3.4	2	1.2	94.8	2.5	13.0	0.5
Engraulidae								
Anchoa mitchilli	3	5.2	3	1.8	3.5	0.1	10.0	0.4
Anchoa spp.	2	3.4	2	1.2	1.5	0.0	4.4	0.2
Gadidae								
Urophycis regia	1	1.7	1	0.6	11.4	0.3	1.6	0.1
Lophiidae								
Lophius americanus	1	1.7	1	0.6	3.2	0.1	1.2	0.0
Achiridae								
Trinectes maculatus								
Paralichthyidae	2	3.4	3	1.8	15.7	0.4	7.8	0.3
Etropus microstomus								
Pleuronectidae	3	5.2	4	2.5	9.8	0.3	14.0	0.5
Unidentified flatfish	1	1.7	2	1.2	10.7	0.3	2.6	0.1
Moronidae								
Morone saxatilis	1	1.7	1	0.6	61.2	1.6	3.9	0.1
Sciaenidae								
Cynoscion nebulosus	1	1.7	1	0.6	0.0	0.0	1.1	0.0
Cynoscion regalis	5	8.6	11	6.7	203.9	5.4	105.1	3.9
Cynoscion spp.	1	1.7	1	0.6	1.6	0.0	1.1	0.0
Micropogonias undulatus	11	19.0	15	9.2	849.2	22.7	604.9	22.4
Unidentified sciaenid	1	1.7	1	0.6	0.0	0.0	1.1	0.0
Unidentified teleost	9	15.5	8	4.9	588.4	15.7	320.1	11.8
Elasmobranchs								
Rajidae								
Raja eglanteria	4	6.9	4	2.5	742.3	19.8	153.7	5.7

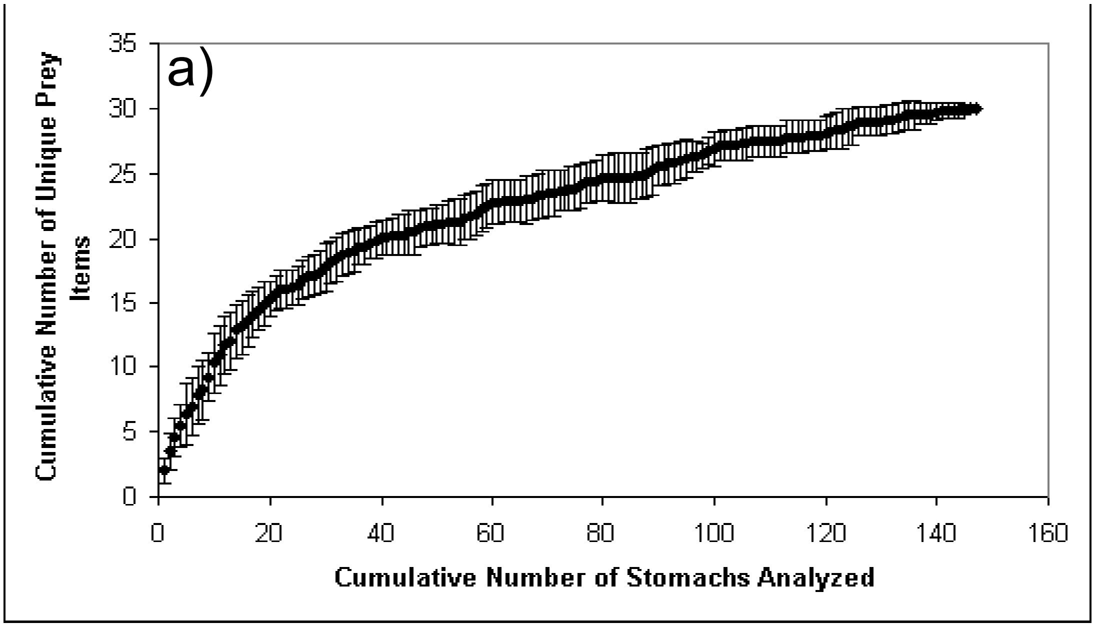
Prey Item	No. Stom.	%F	No. Items	%N	Wet Wt. (g)	%W	IRI	%IRI
Unidentified rajid	3	5.2	3	1.8	103.5	2.8	23.8	0.9
Rajid egg case	5	8.6	6	3.7	50.3	1.3	43.3	1.6
Unidentified batoid	1	1.7	1	0.6	1.4	0.0	1.1	0.0
Unidentified elasmobranch	1	1.7	1	0.6	294.5	7.9	14.6	0.5
Unidentified fish	1	1.7	0	0.0	5.2	0.1	0.2	0.0
Bivalves								
Spissula solidissima	1	1.7	1	0.6	26.7	0.7	2.3	0.1
Cephalopods								
Loligonidae	1	1.7	1	0.6	0.1	0.0	1.1	0.0
Loligo pealei	2	3.4	8	4.9	6.1	0.2	17.5	0.6
Loligo spp.	5	8.6	6	3.7	38.2	1.0	40.5	1.5
Lolliguncula brevis	1	1.7	1	0.6	4	0.1	1.2	0.0
Plants								
Aghardiella spp.	1	1.7	1	0.6	0.1	0.0	1.1	0.0
Other								
Unidentified biological matter	15	25.9	5	3.1	19.8	0.5	93.0	3.4

2001-2002 size class III samples (n = 58) did not reach an asymptote. Some, but not all of the prey items have been listed by this data set. The curve of the 147 records of class III stomachs for the entire data set seemed to approach an asymptote; this sample likely sufficiently represented the diet of this size group (Figures 10a, b).

For the largest size class of sharks (≥ 100 cm PCL), crustaceans occurred less frequently (15.9%). Teleosts were found in 58.3% of stomachs, and elasmobranchs were found in 30.3% of stomachs examined. Cephalopods were consumed by 13.6% sharks with food in their stomachs. Unidentified teleosts (32.6%) and unidentified rajids (12.9%) occurred most frequently (Table 11). Only eight animals in this size class were caught in 2001-2002. Of these, croaker was found in three of them and had the highest weight values (50.1%), followed by unidentified elasmobranch (35.8%) (Table 12). Category %IRI values were 51.2, 18.2, 26.3 for teleosts, crustaceans, and elasmobranchs, respectively (Table 6). Weight and abundance of elasmobranchs were larger than those of size class III. Crustaceans still occurred frequently, but weighed less than other prey categories (Figure 11). The cumulative prey curve for the eight current shark stomach samples did not approach an asymptote and is clearly an inadequate sample size; however, the curve generated using the 132 samples from the complete data set does appear to reach or approach an asymptote and is likely an adequate representation of the large sandbar sharks' diet (Figures 12a, b).

Figure 10a: Cumulative prey curve for size class III sandbar sharks (81-100 cm PCL) for all data, including archival records and 2001-2002 samples (n = 147).

Figure 10b: Cumulative prey curve for size class III sandbar sharks (81-100 cm PCL) from 2001-2002 samples (n = 58).


a)
Cumulative Number of Unique Prey Items
Cumulative Number of Stomachs Analyzed
0
5
10
15
20
25
30
35
0
20
40
60
80
100
120
140
160

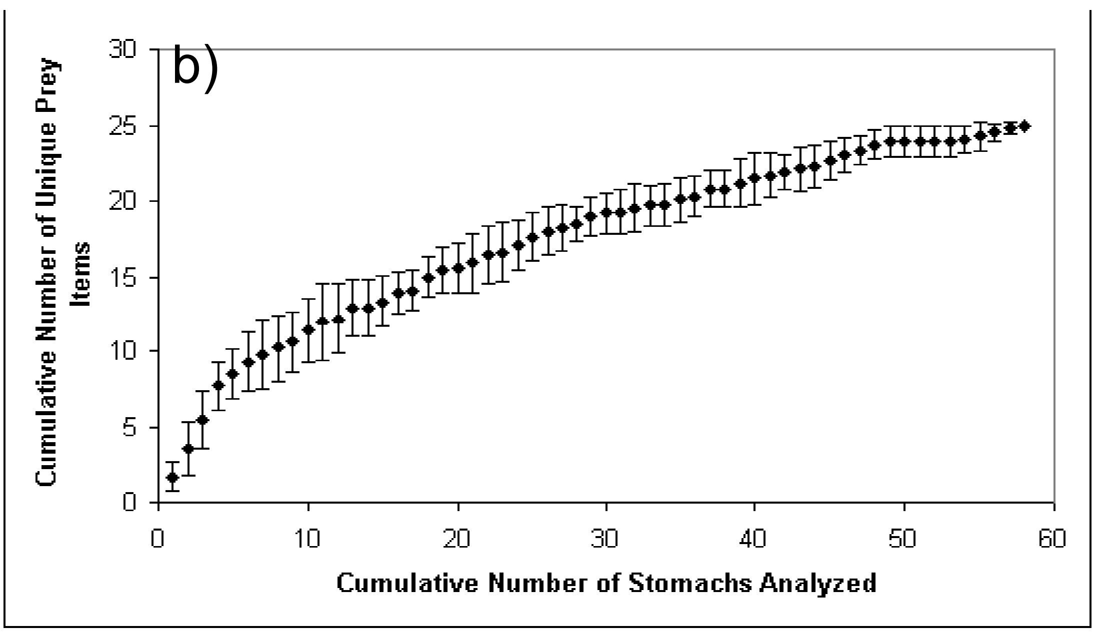
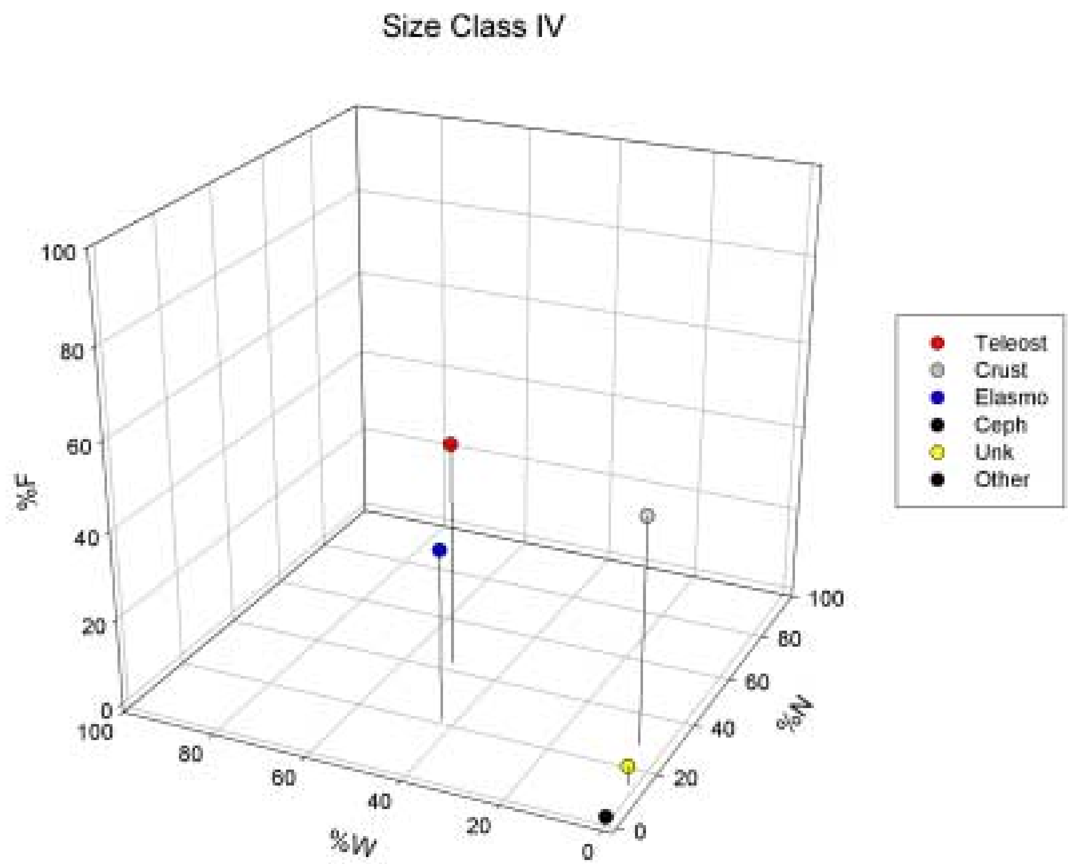

b)
Cumulative Number of Unique Prey Items
Cumulative Number of Stomachs Analyzed
0
5
10
15
20
25
30
0
10
20
30
40
50
60

Table 11: Prey item scientific and common names with frequency of occurrence (F) values and percentages for 132 sandbar sharks greater than 100 cm PCL.

Prey Item	Common Name	F	%F
Crustaceans			
Squillidae			
Squilla empusa	mantis shrimp	5	3.8
Portunidae			
Callinectes sapidus	blue crab	2	1.5
Carcinus maenus	green crab	1	0.8
Ovalipes ocellatus	lady crab	6	4.5
Unidentified portunid	swimming crab	2	1.5
Majidae	spider crab	5	3.8
Unidentified crab		2	1.5
Paguridae			
Pagurus spp.	hermit crab	1	0.8
Teleosts			
Anguillidae			
Anguilla spp.	eel	1	0.8
Congridae			
Conger oceanicus	conger eel	1	0.8
Clupeidae			
Brevoortia spp.	menhaden	2	1.5
Gadidae			
Urophycis spp.	hake	1	0.8
Ophidiidae	cusk eels	1	0.8
Pomatomidae			
Pomatomus saltatrix	bluefish	8	6.1
Rachycentridae			
Rachycentron canadum	cobia	1	0.8
Sciaenidae			
Bairdiella chrysoura	silver perch	1	0.8
Leiostomus xanthurus	spot	1	0.8
Micropogonias undulatus	croaker	4	3.0
Unidentified sciaenid	drum	2	1.5
Serranidae		5	3.8
Centropristis striata	black sea bass	2	1.5
Uranoscopidae			
Astroscopus guttatus	northern stargazer	5	3.8
Achiridae			
Trinectes maculatus	hogchoker	1	0.8
Unidentified flatfish		1	0.8
Triglidae		8	6.1
Prionotus carolinus	northern searobin	2	1.5
Unidentified teleost		43	32.6
Elasmobranchs			
Carcharhinidae			
Carcharhinus plumbeus	sandbar shark	1	0.8
Dasyatidae			
Dasyatis spp.	stingray	1	0.8
Unidentified dasyatid		1	0.8

Prey Item	Common Name	F	%F
Rajidae			
Leucoraja erinacea	little skate	2	1.5
Raja eglanteria	clearnose skate	4	3.0
Rajid egg case	skate egg case	2	1.5
Unidentified rajid	skate	17	12.9
Rhinopteridae			
Rhinoptera bonasus	cownose ray	1	0.8
Triakidae			
Mustelus canis	smooth dogfish	1	0.8
Unidentified batoid	skates/stingrays	6	4.5
Unidentified elasmobranch	skates/stingrays/sharks	2	1.5
Molluscs			
Cephalopods			
Loligonidae			
Loligo pealei	long-finned squid	8	6.1
Unidentified cephalopod		10	7.6
Bivalves			
Mytilidae	mussels	1	0.8
Gastropods			
Littorina spp.	periwinkle	2	1.5
Nassariidae	dog whelks	1	0.8
Nudibranchia	nudibranchs	1	0.8
Unidentified mollusc		1	0.8
Plants			
Unidentified plant		1	0.8
Other			
Limulus polyphemus	horseshoe crab	1	0.8
Polychaete		1	0.8
Unidentified biological matter		3	2.3

Figure 11: Number (%N), weight (%W), and frequency (%F) indices for size class IV (> 100 cm PCL) sandbar sharks from 2001-2002 samples (n = 8).



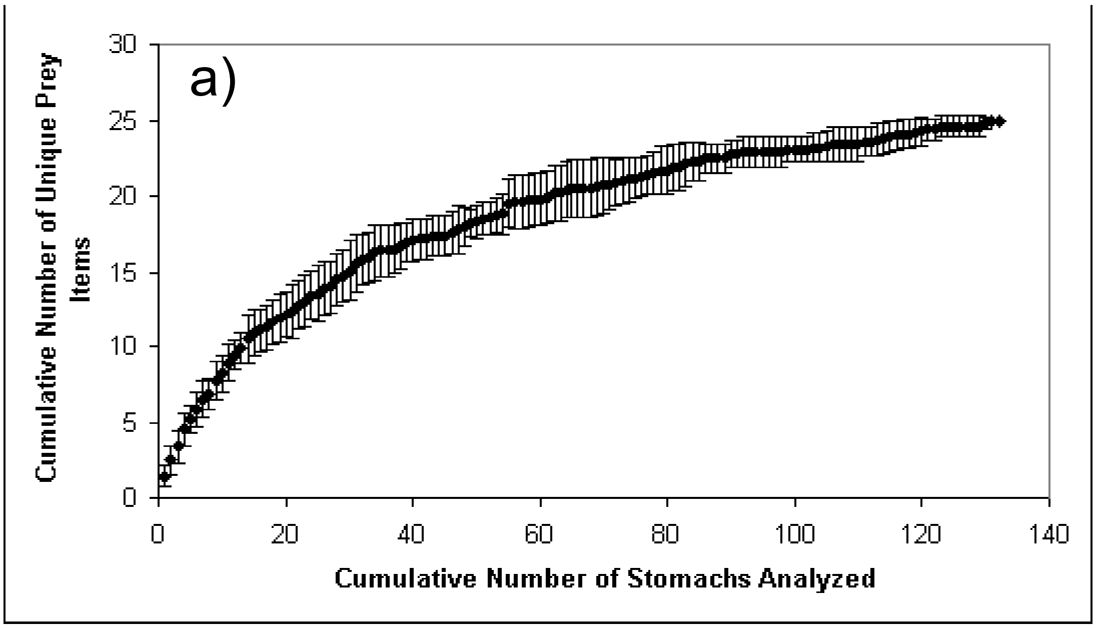
Size Class IV
%F
%W
%N
100
80
60
40
20
0
Teleost
Crust
Elasmo
Ceph
Unk
Other

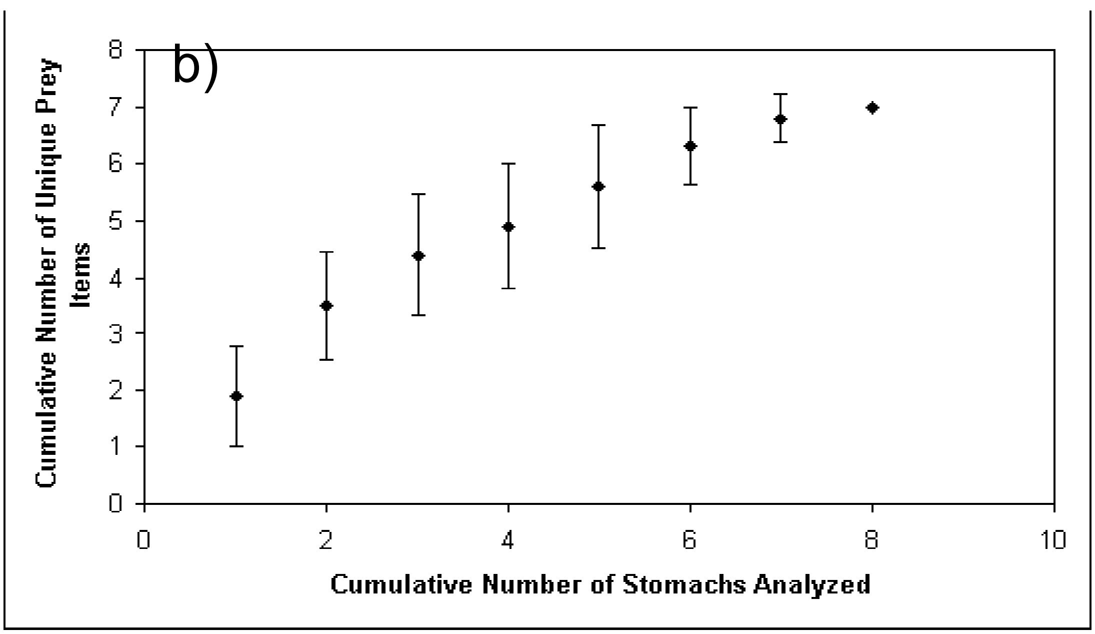
Table 12: Prey item frequency (F), number (N), wet weight (W), and index of relative importance (IRI) values and percentages for 8 sandbar sharks > 100 cm PCL.

Prey Item	No. Stom.	%F	No. Items	%N	Wet wt. (g)	%WW	IRI	%IRI
Crustaceans								
Squilla empusa	2	25.0	2	14.3	9.8	2.0	406.1	8.5
Ovalipes ocellatus	1	12.5	1	7.1	9.2	1.8	112.3	2.4
Portunus spp.	1	12.5	1	7.1	4.8	1.0	101.3	2.1
Teleosts								
Sciaenidae								
Micropogonias undulatus	3	37.5	4	28.6	250.6	50.1	2950.2	61.7
Serranidae								
Centropristis striata	1	12.5	2	14.3	3.7	0.7	187.8	3.9
Elasmobranchs								
Rajidae								
Raja eglanteria	1	12.5	1	7.1	23.2	4.6	147.3	3.1
Unidentified rajid	1	12.5	1	7.1	12.2	2.4	119.8	2.5
Unidentified elasmobranch	1	12.5	1	7.1	179.3	35.8	537.4	11.2
Other								
Unidentified biological matter	2	25.0	1	7.1	7.4	1.5	215.6	4.5

Figure 12a: Cumulative prey curve for size class IV (> 100 cm PCL) sandbar sharks from all data, including archival records and 2001-2002 samples (n = 132).

Figure 12b: Cumulative prey curve for size class IV (> 100 cm PCL) sandbar sharks from 2001-2002 samples (n = 8).


a)
Cumulative Number of Unique Prey Items
Cumulative Number of Stomachs Analyzed
0
5
10
15
20
25
30
0
20
40
60
80
100
120
140


b)
Cumulative Number of Unique Prey Items
Cumulative Number of Stomachs Analyzed
0
1
2
3
4
5
6
7
8
0
2
4
6
8
10

IRI data for broad prey categories changed with increasing shark size. Bony fishes increased in importance from size class I to II, and then gradually decreased from II to III and III to IV (Figure 13). Crustaceans decreased in importance from smaller sharks to larger sharks. Elasmobranchs increased in importance with increasing shark size, as did unknown. Cephalopods had a small increase from class II to III, but exhibited no major trend. The small number of samples for the largest size class in this subset of data (n = 8) might suggest that the trends in the IRI data were inconclusive. However, %F values for the entire data set reflected similar trends (Figure 14). Teleosts increased in importance from class I to class II, remained the same from II to III, and decreased from III to IV. Crustaceans decreased in importance from class I, remained approximately the same between II and III, and decreased further from III to IV. Elasmobranchs and cephalopods exhibited the reverse trend, increasing with increasing shark size. Unknown remained the same for the first three size classes and decreased for class IV. Classes II and III were functionally the same in terms of %F.

Size classes I and IV had the least overlap in diet according to both the Schoener and Simplified Morisita indices, and values were especially low when weight proportions were used in the calculations (Table 13). A negative Schoener value, which was obtained when the index was calculated using average weight, was rounded to 0.00. This negative value was likely due to the broad prey categories used in the calculations. When frequency percentages from the 2001-2002 data were used, classes I and II and classes II and III had the highest degree of overlap for both the Schoener and the Simplified Morisita indices. Schoener and

Figure 13: Index of relative importance (IRI) percentages for five prey types (teleost, crustacean, elasmobranch, cephalopod, and unknown) and four size classes of sandbar sharks (< 61, 61-80, 81-100, and > 100 cm PCL).

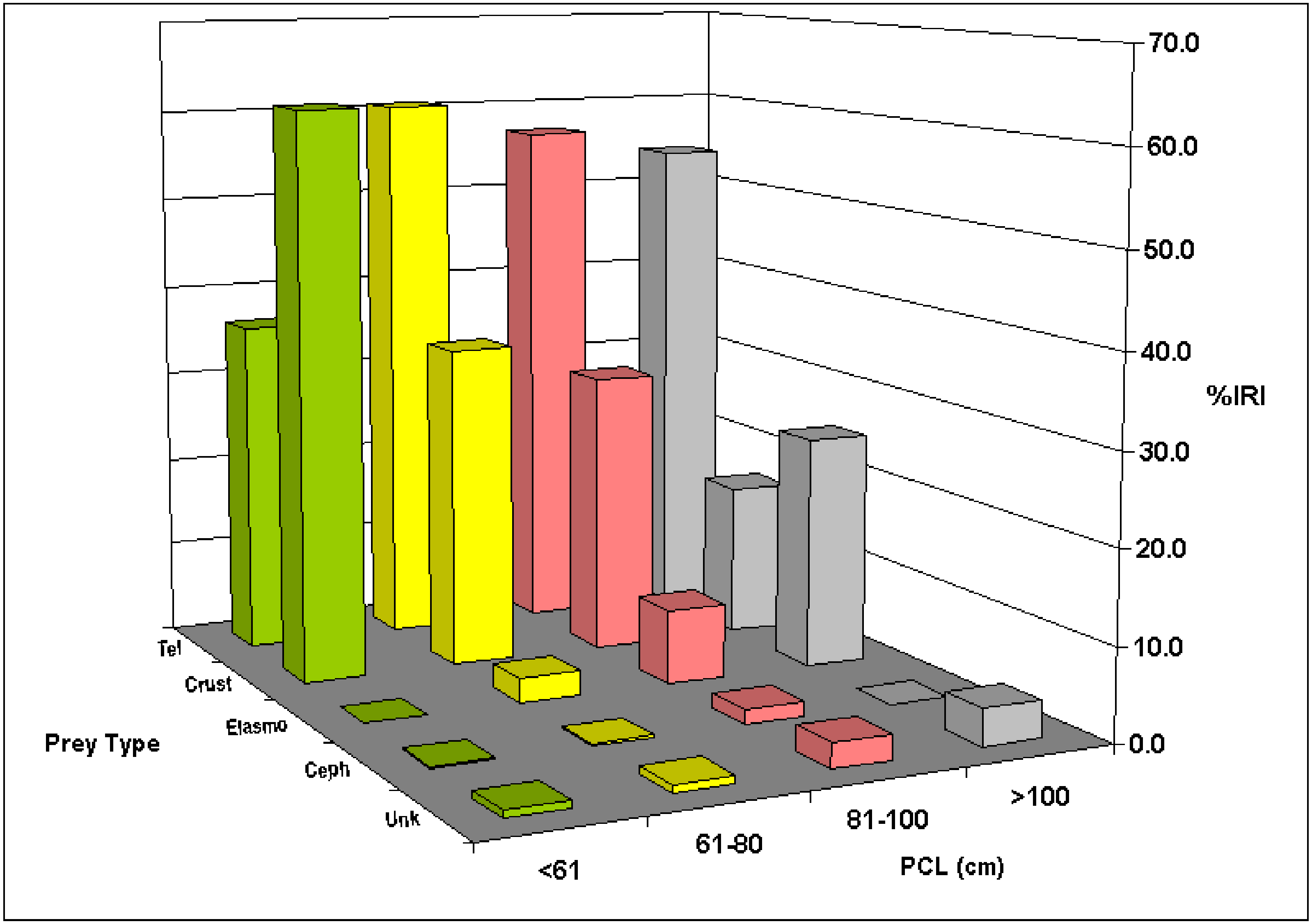
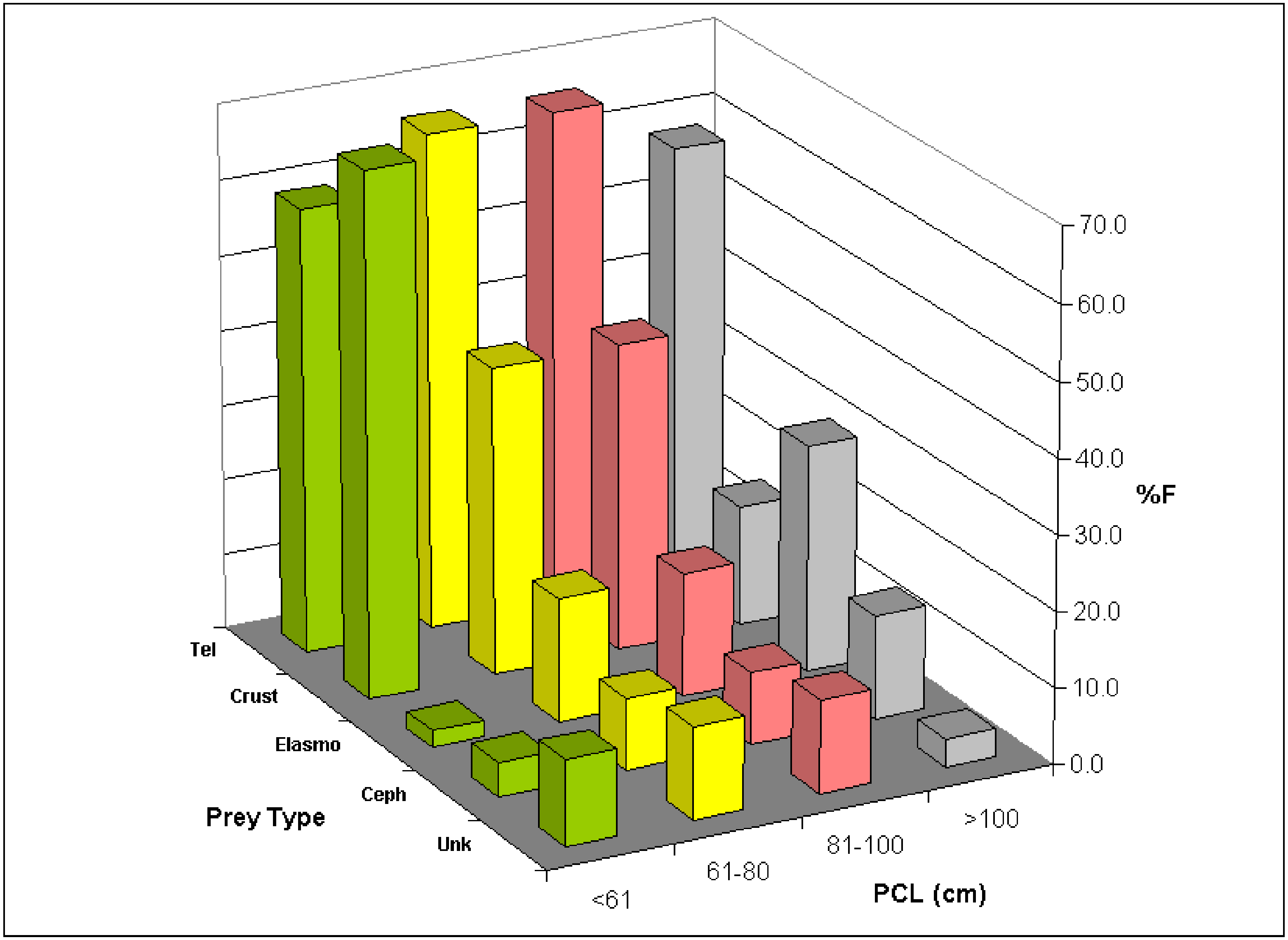

70.0
60.0
50.0
40.0
30.0
20.0
10.0
0.0
%IRI
Tel
Crust
Elasmo
Ceph
Unk
Prey Type
<61
61-80
81-100
>100
PCL (cm)

Figure 14: Frequency (F) percentages for five prey types (teleost, crustacean, elasmobranch, cephalopod, and unknown) and four size classes of sandbar sharks (< 61, 61-80, 81-100, and > 100 cm PCL).



70.0
60.0
50.0
40.0
30.0
20.0
10.0
0.0
%F
Tel
Crust
Elasmo
Ceph
Unk
Prey Type
<61
61-80
81-100
>100
PCL (cm)

Table 13: Index of diet overlap values by size class: I = ≤ 60 cm PCL, II = 61-80 cm PCL, III = 81-100 cm PCL, IV = ≥ 100 cm PCL. Red indicates greatest overlap value for each calculation method; green indicates least overlap.

	Size Classes					
Index Used	I and II	II and III	III and IV	I and III	I and IV	II and IV
Schoener using avg W	0.51	0.84	0.32	0.54	-0.06	0.41
Schoener using %IRI	0.74	0.91	0.79	0.65	0.50	0.74
Schoener using %W	0.69	0.81	0.89	0.52	0.42	0.70
Schoener using %F	0.84	0.83	0.68	0.67	0.53	0.66
Schoener using %N	0.86	0.88	0.78	0.82	0.68	0.79
Schoener using %F (all data)	0.71	0.92	0.70	0.72	0.50	0.68
Simplified Morisita using %IRI	0.88	0.99	0.93	0.81	0.61	0.86
Simplified Morisita using %W	0.85	0.92	0.98	0.61	0.45	0.81
Simplified Morisita using %F	0.98	0.98	0.94	0.95	0.85	0.92
Simplified Morisita using %F (all data)	0.92	0.99	0.91	0.93	0.71	0.91

Table 14: Shannon-Wiener prey diversity index by size class

PCL (cm)	Prey Diversity
≤ 60	0.593
61-80	0.620
81-100	0.695
≥ 100	0.694

Simplified Morisita index values calculated using frequencies from the entire data set indicated that classes II and III had the highest amount of overlap. IRI data yielded highest overlap between classes II and III for both tests, as did %N for the Schoener index. According to all the iterations of the various indices, diets of classes I and IV overlapped the least, and the most overlap existed between the middle two size classes. Shannon-Wiener prey diversity values showed increasing prey diversity from classes I to II and II to III, followed by a slight decrease from class III to class IV (Table 14).

A plot of IRI values generated by correspondence analysis showed the size groups spread out along principal component one (Figure 15). Crustaceans grouped with the smallest size class, and elasmobranchs were closest to the largest size class. Size class II fell between crustaceans and bony fishes, and size class III was plotted closest to bony fishes. Cephalopods were far removed from the group along component two. A chi-squared test for size class and three prey groups (Teleostei, Crustacea, and Elasmobranchii) was significant ($p < 0.0005$, df = 6), with the main source of variation coming from the crustacean and elasmobranch prey groups in size classes I and IV. CA for frequency data showed similar results, with size class extending along the first component. Size classes II and III were at almost the same position along component one. Cephalopods were closer to the largest size class, and unknown fell between the two smallest size classes (Figure 16).

Elasmobranchs gradually entered the diet as sharks grew larger, as seen in Figure 17. At approximately 160 cm PCL, there was a 50 percent chance that

Figure 15: Biplot of size class (< 61, 61-80, 81-100, > 100 cm PCL) and prey group (teleost, crustacean, cephalopod, elasmobranch, and unknown) principal components (PCs) for component 1 and component 2 of a correspondence analysis using %IRI data.

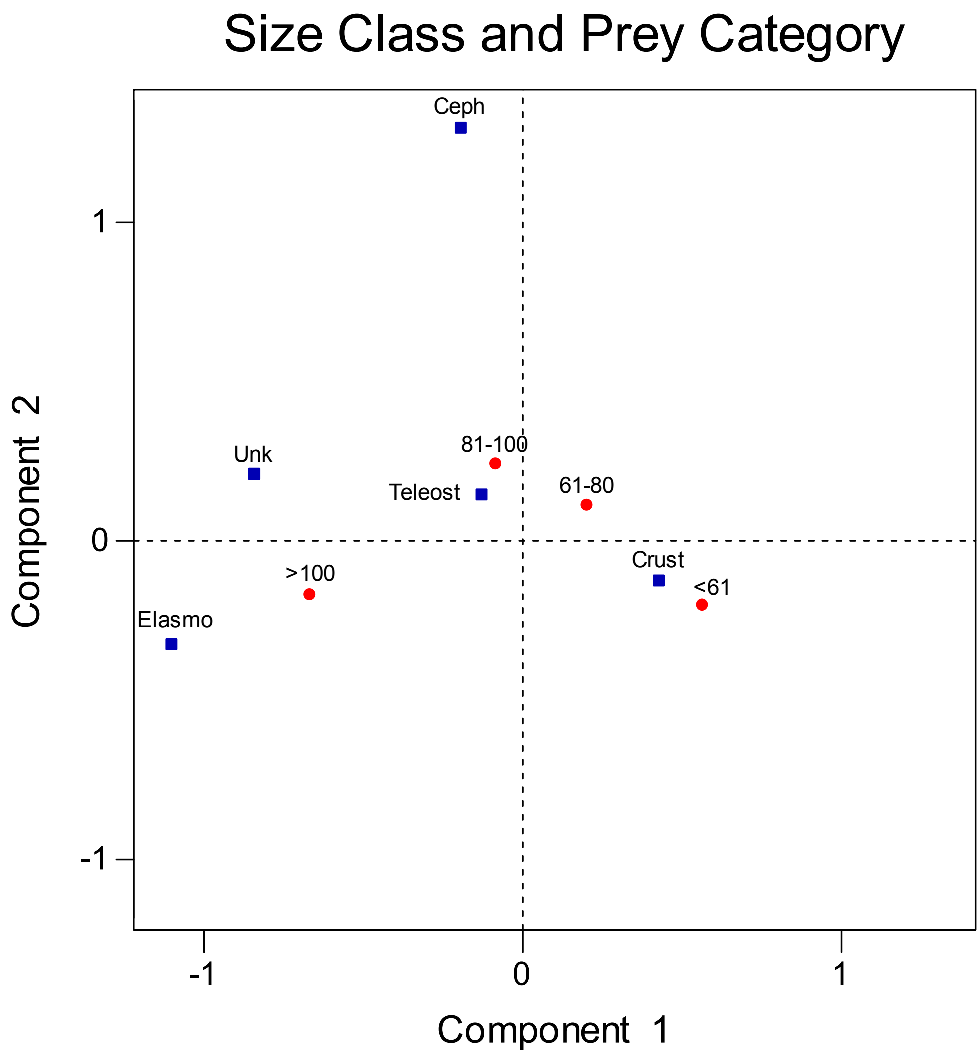
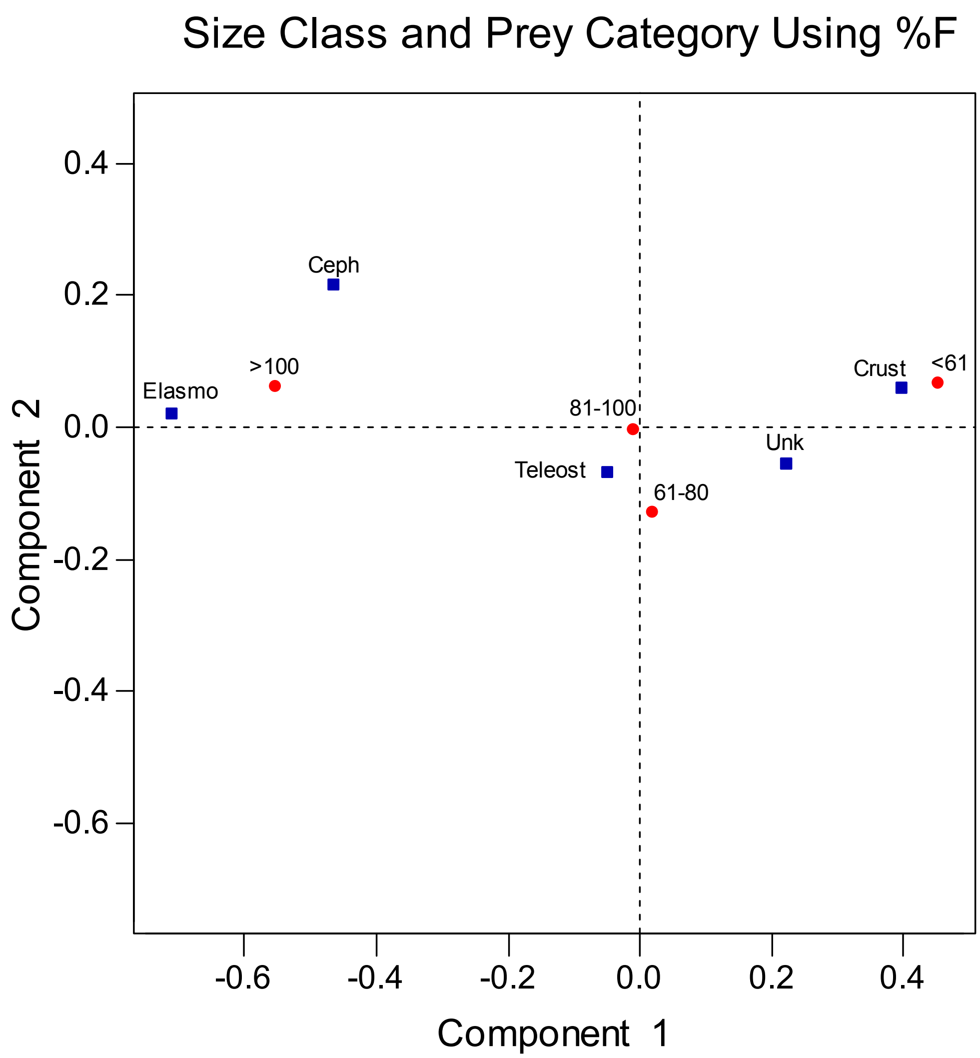

Size Class and Prey Category
Ceph
Unk
81-100
Teleost
61-80
Crust
<61
>100
Elasmo
1
0
-1
-1
0
1
Component 2
Component 1

Figure 16: Biplot of size class (< 61, 61-80, 81-100, > 100 cm PCL) and prey group (teleost, crustacean, cephalopod, elasmobranch, and unknown) principal components (PCs) for component 1 and component 2 of a correspondence analysis using %F data.



Size Class and Prey Category Using %F
Component 2
Component 1
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.6
-0.4
-0.2
0.0
0.2
0.4
Ceph
>100
Elasmo
81-100
Teleost
61-80
Unk
Crust
<61

a shark would have an elasmobranch prey item in its stomach. This progressive change was also observed in the regression of jaw bite radius to shark PCL (R^2 = 0.9064; $p < 0.0005$; Figure 18). Estimates of upper bite radius, generated using the above regression equation, were plotted on the same graph as probability of elasmobranch in diet, revealing a mirror image (Figure 19).

Location

Predominance of prey groups varied among five longline stations (Figure 20). Shark stomachs from Wreck Island (W) on Virginia's Eastern Shore (Figure 4) had the highest frequency of crustaceans. Kiptopeke (K) and Middleground (M), which are Bay stations, had fewer occurrences of crustaceans in shark diet, but still had values greater than the coastal station Virginia Beach (V) and the furthest offshore station (Triangle, T). T, on the other hand, had the highest frequencies of cephalopods and elasmobranchs. Fish occurrence in sandbar shark diet was high at V, M, and K, and was lowest at W. Correspondence analysis showed associations of crustaceans with station W and elasmobranchs with station T. V was close to T in principal component 1, and M fell between W and K on the plot (Figure 21).

Frequency of prey category varied for stations (both gillnet and longline) grouped by station type—Eastern Shore, Bay, and Coastal. (Figure 22). Crustaceans were more frequent at Eastern Shore stations, and elasmobranchs and cephalopods occurred more often in coastal shark stomachs. Bony fishes

Figure 17: Presence (probability = 1) and absence (probability = 0) of elasmobranch in diet versus precaudal length (PCL) (black dots) with binary logistic regression of probability of elasmobranch occurrence in diet (red dots).

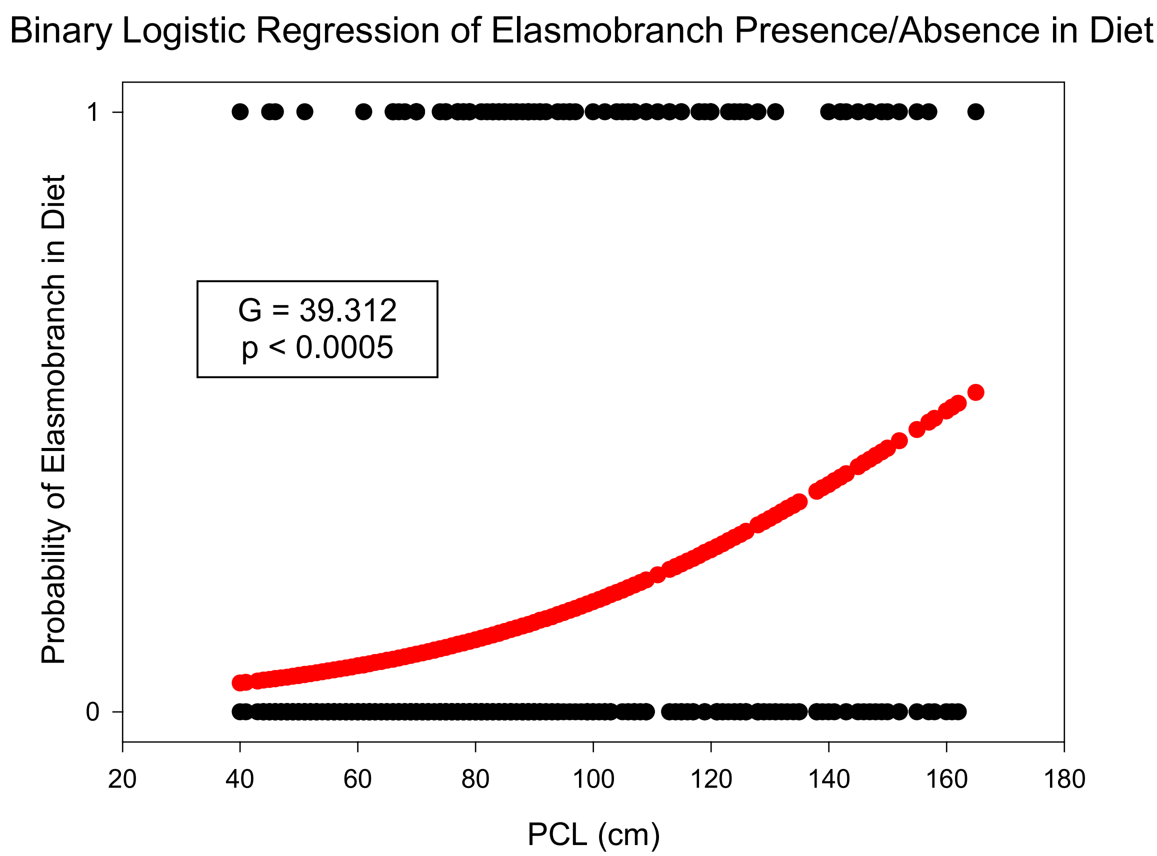
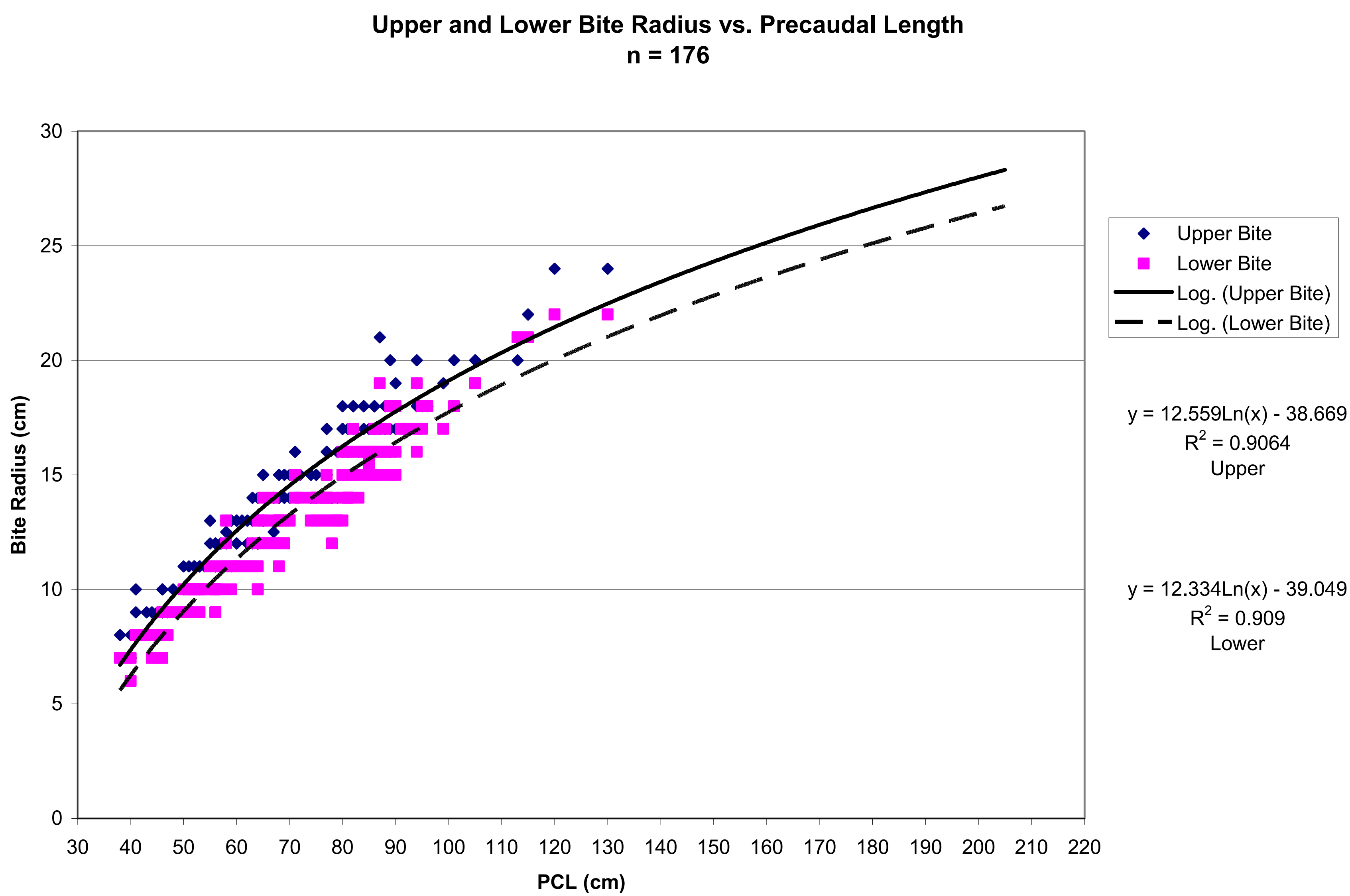

Binary Logistic Regression of Elasmobranch Presence/Absence in Diet
G = 39.312
p < 0.0005
Probability of Elasmobranch in Diet
1
0
20
40
60
80
100
120
140
160
180
PCL (cm)

Figure 18: Nonlinear regression of upper (diamonds) and lower (squares) bite radius (cm) versus precaudal length (PCL) in cm.



Upper and Lower Bite Radius vs. Precaudal Length
n = 176
Bite Radius (cm)
PCL (cm)
0
5
10
15
20
25
30
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
190
200
210
220
Upper Bite
Lower Bite
Log. (Upper Bite)
Log. (Lower Bite)
y = 12.559Ln(x) - 38.669
R2 = 0.9064
Upper
y = 12.334Ln(x) - 39.049
R2 = 0.909
Lower

Figure 19: Probability of elasmobranch in diet versus precaudal length (PCL) from binary logistic regression (red line) and estimated upper jaw bite radius (cm) versus PCL (black line).

Precaudal Length vs. Probability of Elasmobranch in Diet
and Estimated Upper Jaw Bite Radius

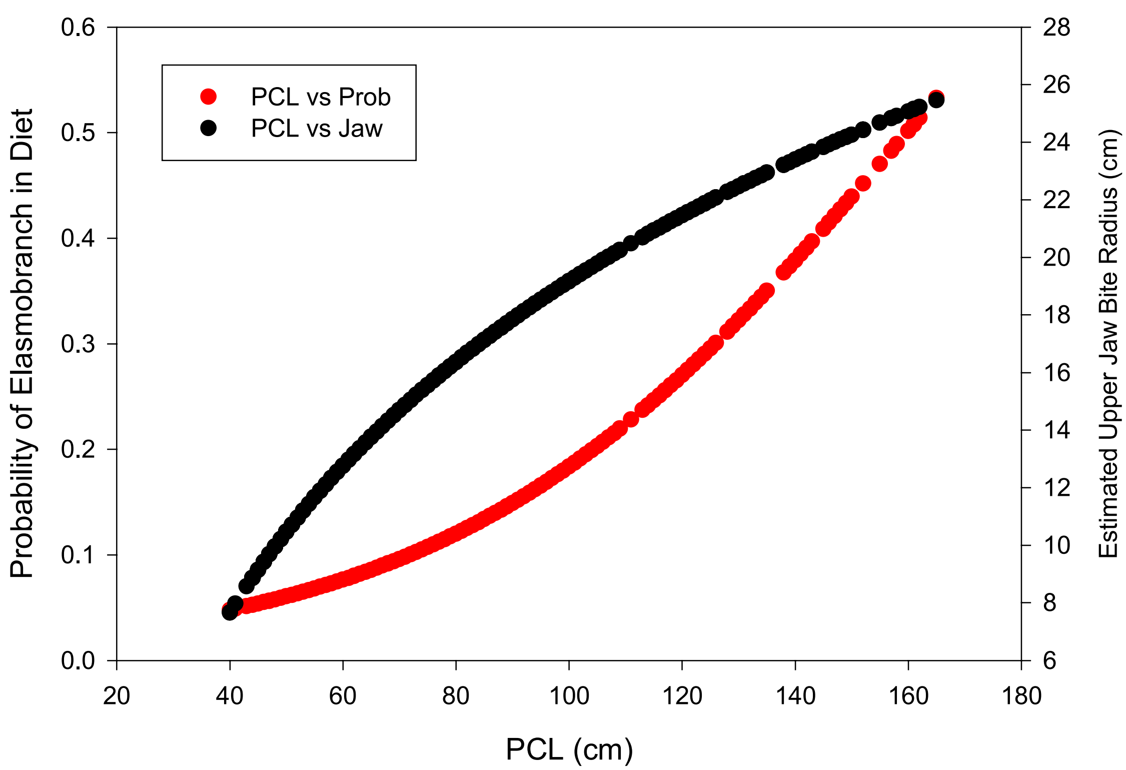
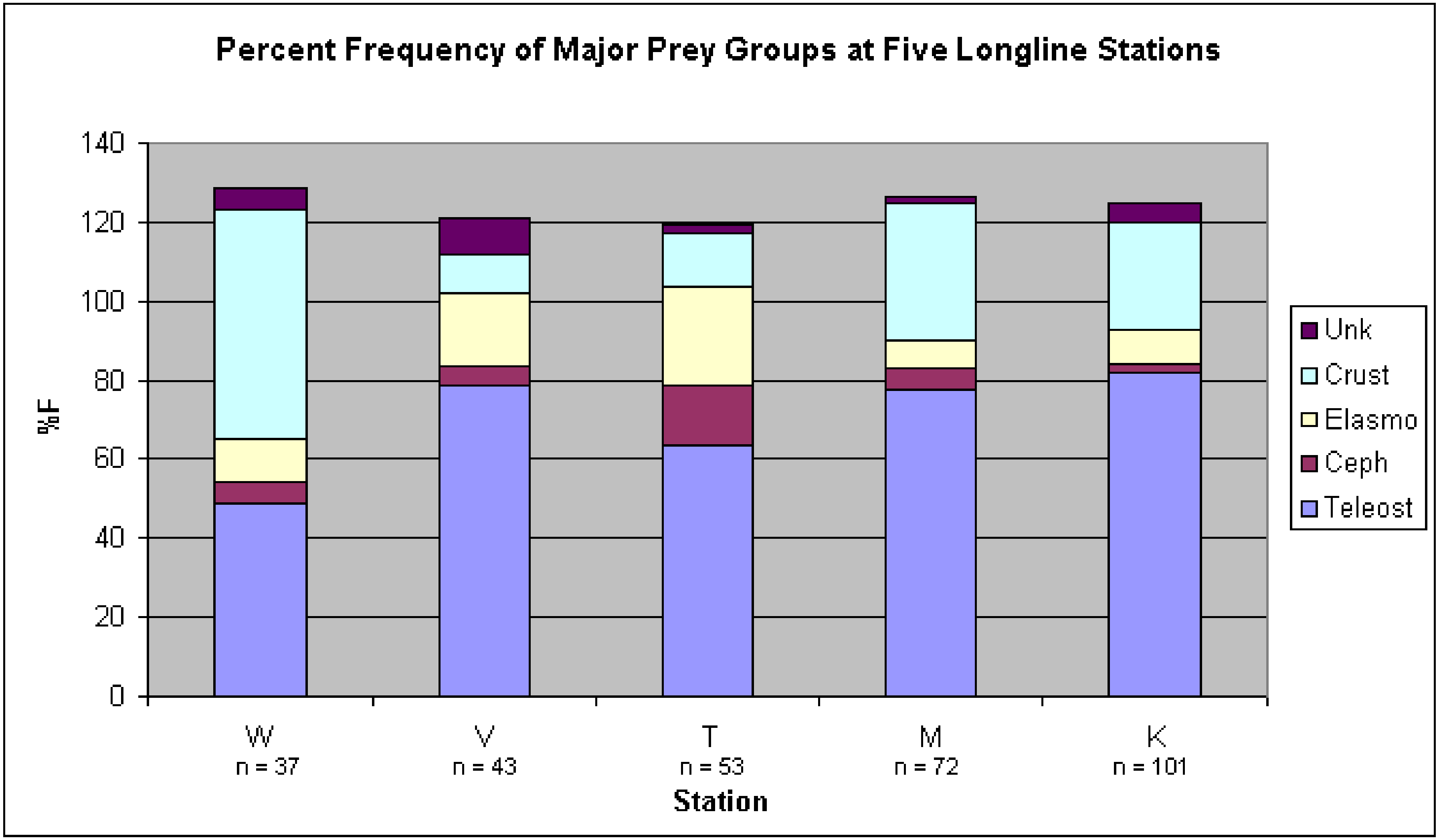
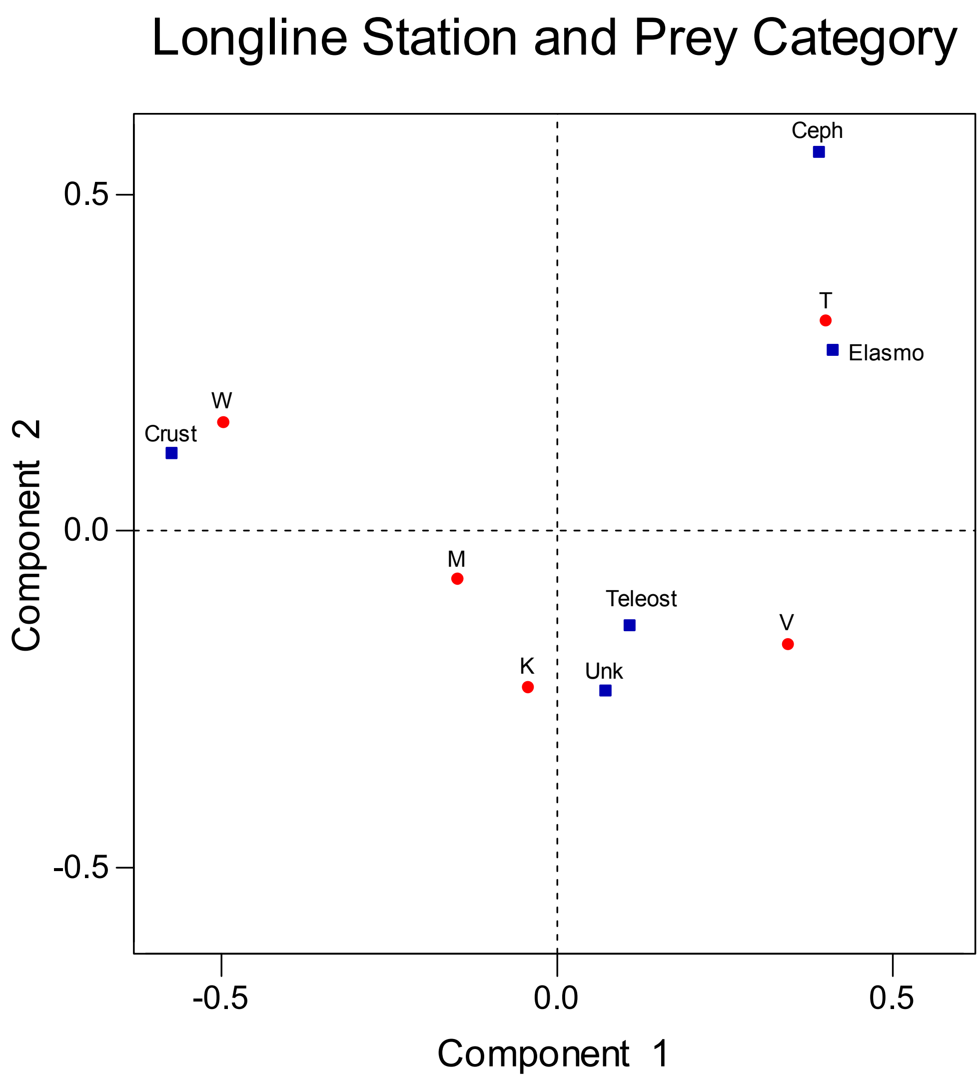


Figure 20: Percent frequency of prey categories (teleost, cephalopod, elasmobranch, crustacean, and unknown) at five longline stations (W, T, V, M, and K).



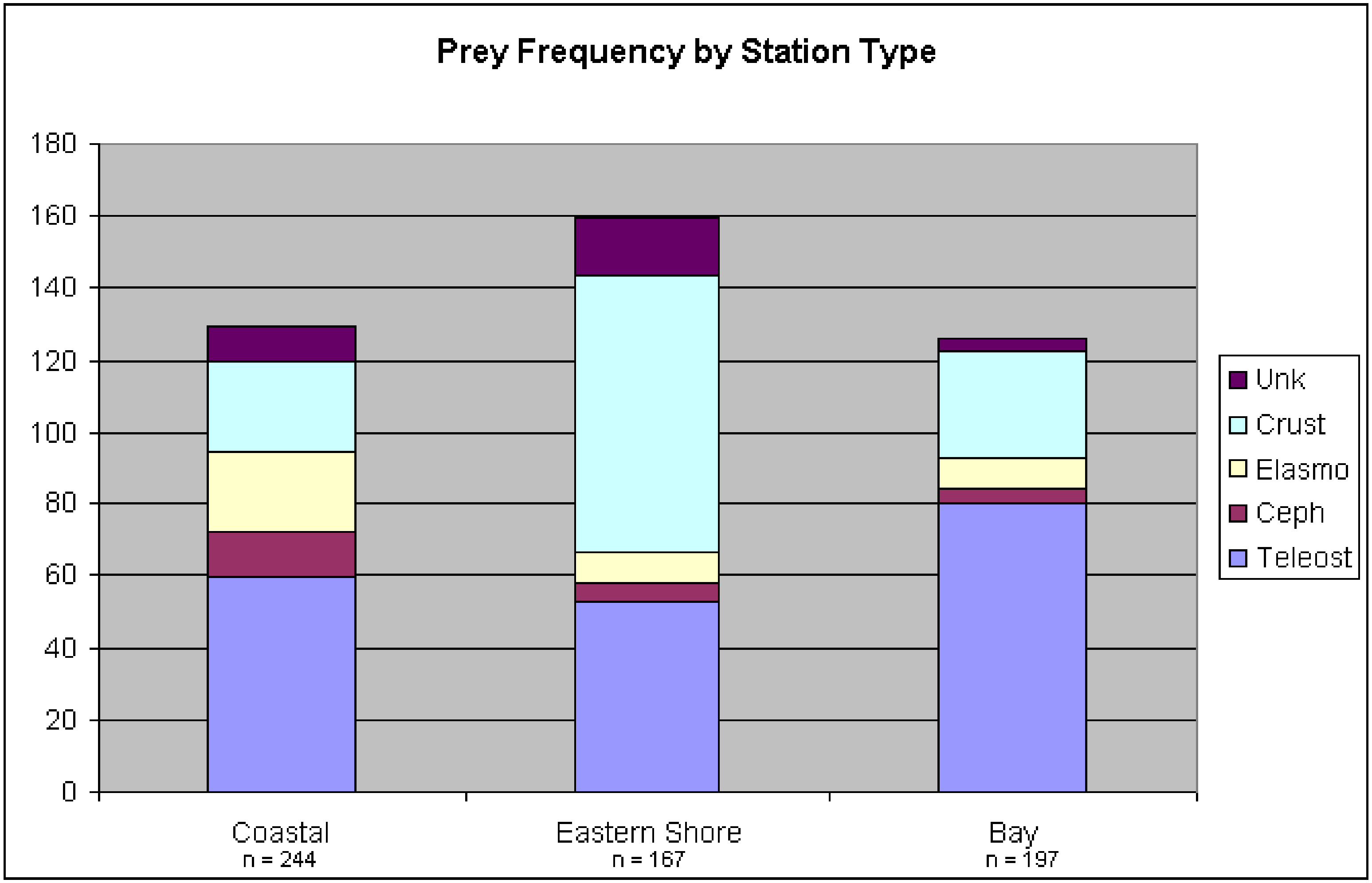
Percent Frequency of Major Prey Groups at Five Longline Stations
%F
140
120
100
80
60
40
20
0
W
n = 37
V
n = 43
T
n = 53
M
n = 72
K
n = 101
Station
Unk
Crust
Elasmo
Ceph
Teleost

Figure 21: Biplot of longline station (W, T, V, M, and K) and prey group (teleost, crustacean, cephalopod, elasmobranch, and unknown) principal components (PCs) for component 1 and component 2 of a correspondence analysis using %F data.



Longline Station and Prey Category
Ceph
T
Elasmo
W
Crust
M
Teleost
V
K
Unk
0.5
0.0
-0.5
-0.5
0.0
0.5
Component 2
Component 1

Figure 22: Percent frequency of prey categories (teleost, cephalopod, elasmobranch, crustacean, and unknown) for three types of station (Coastal, Eastern Shore, and Bay).


Prey Frequency by Station Type
180
160
140
120
100
80
60
40
20
0
Coastal
n = 244
Eastern Shore
n = 167
Bay
n = 197
Unk
Crust
Elasmo
Ceph
Teleost

occurred most frequently at Bay stations. Unidentified prey items were found more often in Eastern Shore samples, followed by Coastal then Bay stations. CA showed clear groupings of crustaceans with Eastern Shore sites, cephalopods and elasmobranchs with Coastal sites, and teleosts with Bay sites (Figure 23). Unidentified prey items did not group closely with a station type. Diet of juveniles (< 90 cm PCL) at Bay and Eastern Shore sites was examined more closely. Chi-squared values for comparison of prey categories between Bay and Eastern Shore indicated significant differences in nursery site diet. Bony fishes were more important in Bay stomachs, and crustaceans were more important for Eastern Shore sharks ($p < 0.0005$).

Small juveniles (less than 80 cm PCL) from the Eastern Shore showed variation in crustacean consumption by region. Portunid crabs occurred more frequently in the diet of Wachapreague small juveniles, and mantis shrimp occurred more frequently in the diet of Sand Shoal Inlet sharks ($p < 0.0005$). Machipongo, the middle region, had sharks with intermediate frequencies of portunid crab and mantis shrimp. CA also revealed this regional gradient in crustacean type (Figure 24).

Multiple analysis of variance (MANOVA) was used to check the combined effects of size class and location on sandbar shark diet. MANOVA did not show significant interaction between size class and location at the 10% level. Nor were the factors on their own significant (Table 15).

Figure 23: Biplot of station type (Coastal, Eastern Shore, and Bay) and prey group (teleost, crustacean, cephalopod, elasmobranch, and unknown) principal components (PCs) for component 1 and component 2 of a correspondence analysis using %F data.

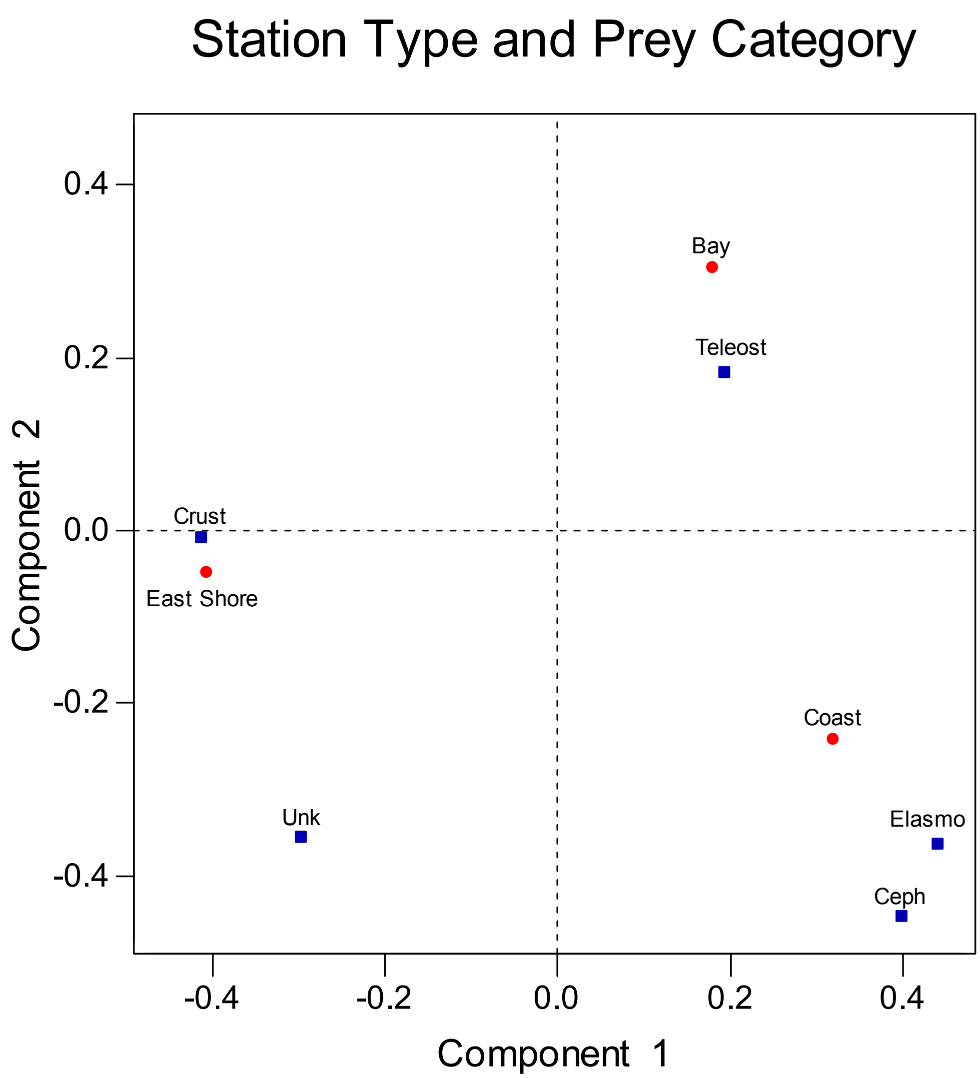

Station Type and Prey Category
Bay
Teleost
Crust
East Shore
Coast
Unk
Elasmo
Ceph
0.4
0.2
0.0
-0.2
-0.4
-0.4
-0.2
0.0
0.2
0.4
Component 2
Component 1

Figure 24: Biplot of Eastern Shore regions—Wachapreague (Wach), Machipongo (Mach), and Sand Shoal Inlet (SSI) —and crustacean type (*Squilla empusa*, portunid crab, unknown, and other) principal components (PCs) for component 1 and component 2 of a correspondence analysis using %F data.

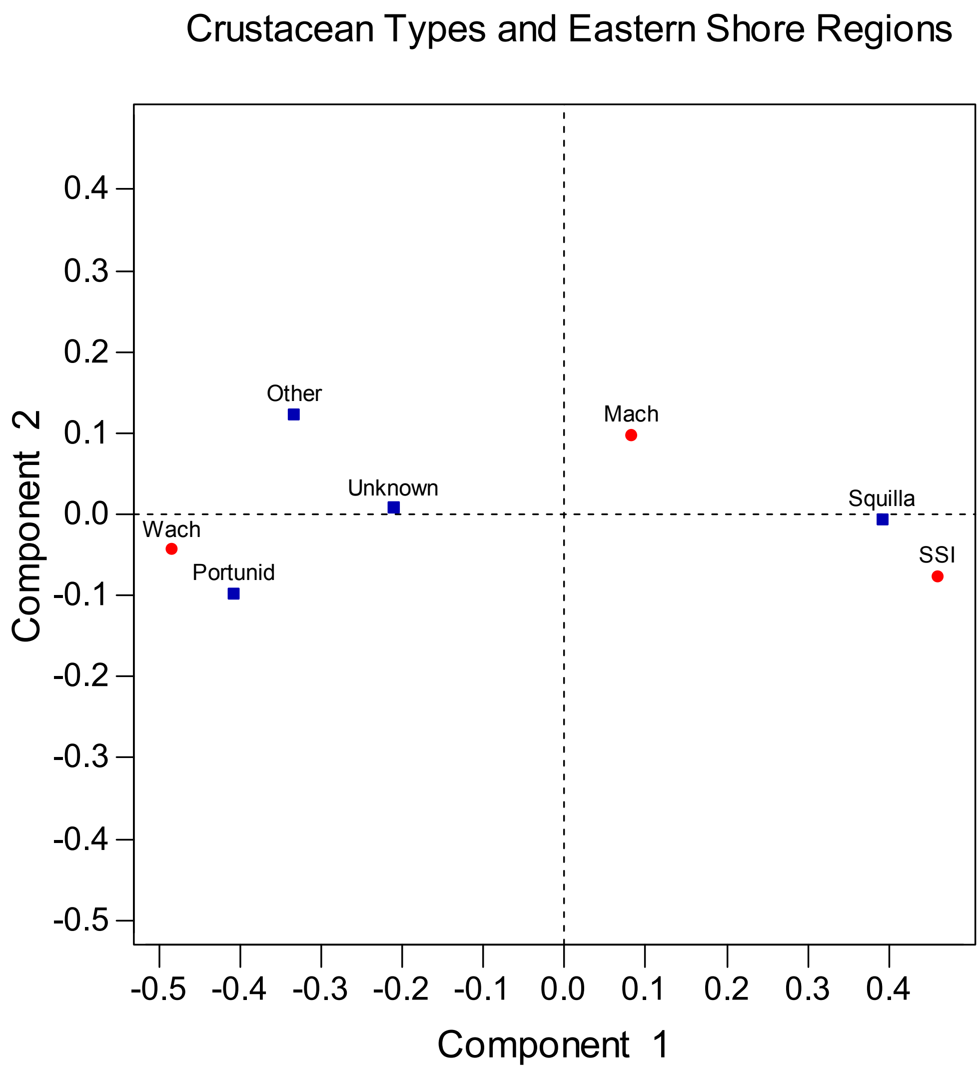

Crustacean Types and Eastern Shore Regions
Other
Mach
Unknown
Squilla
Wach
SSI
Portunid
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
Component 2
-0.5 -0.4 -0.3 -0.2 -0.1 0.0 0.1 0.2 0.3 0.4
Component 1

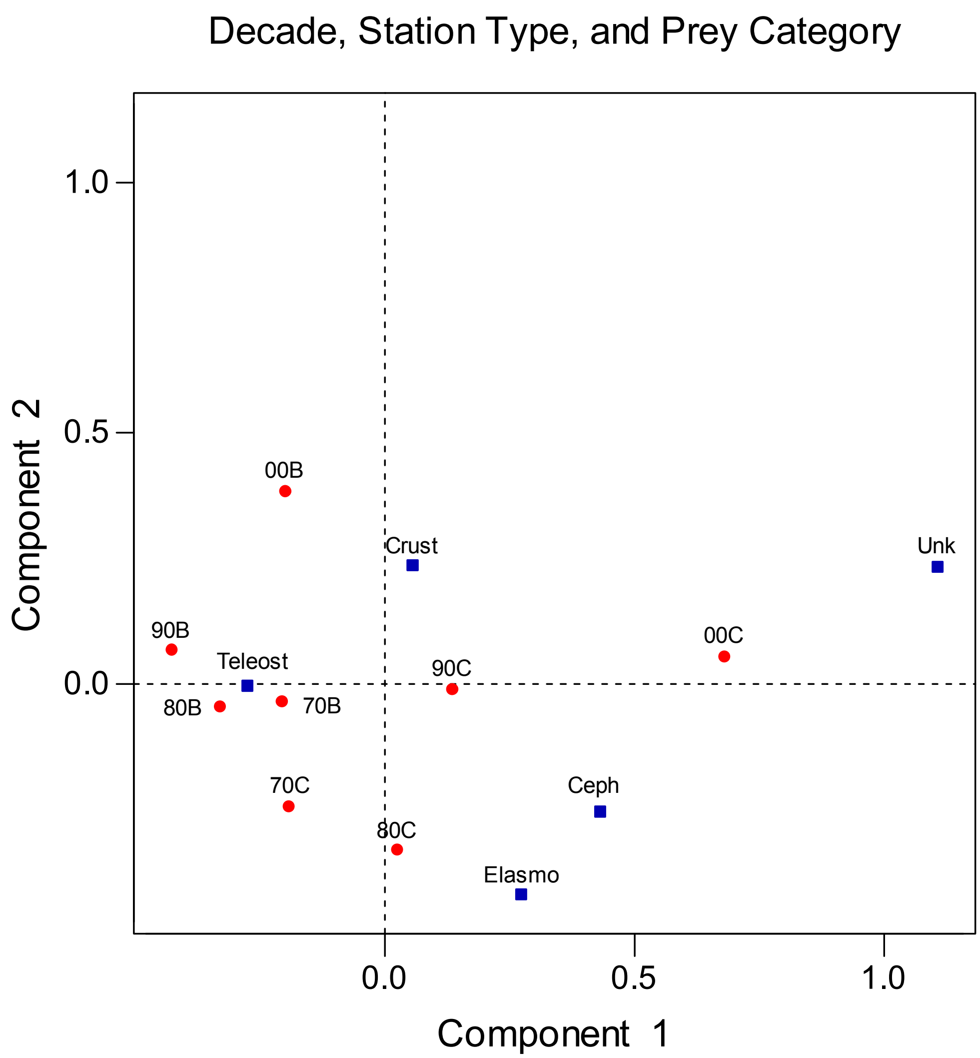
Table 15: Results of a two-way MANOVA with size class and station type as the factors and %F values for 5 prey categories as responses.

Factor/Interaction	Pillai's Trace	F	p-value
Size class	0.73485	$2.217_{5,4}$	0.230
Station Type	0.81018	$3.414_{5,4}$	0.129
Size x Station	0.52681	$0.891_{5,4}$	0.560

Decade

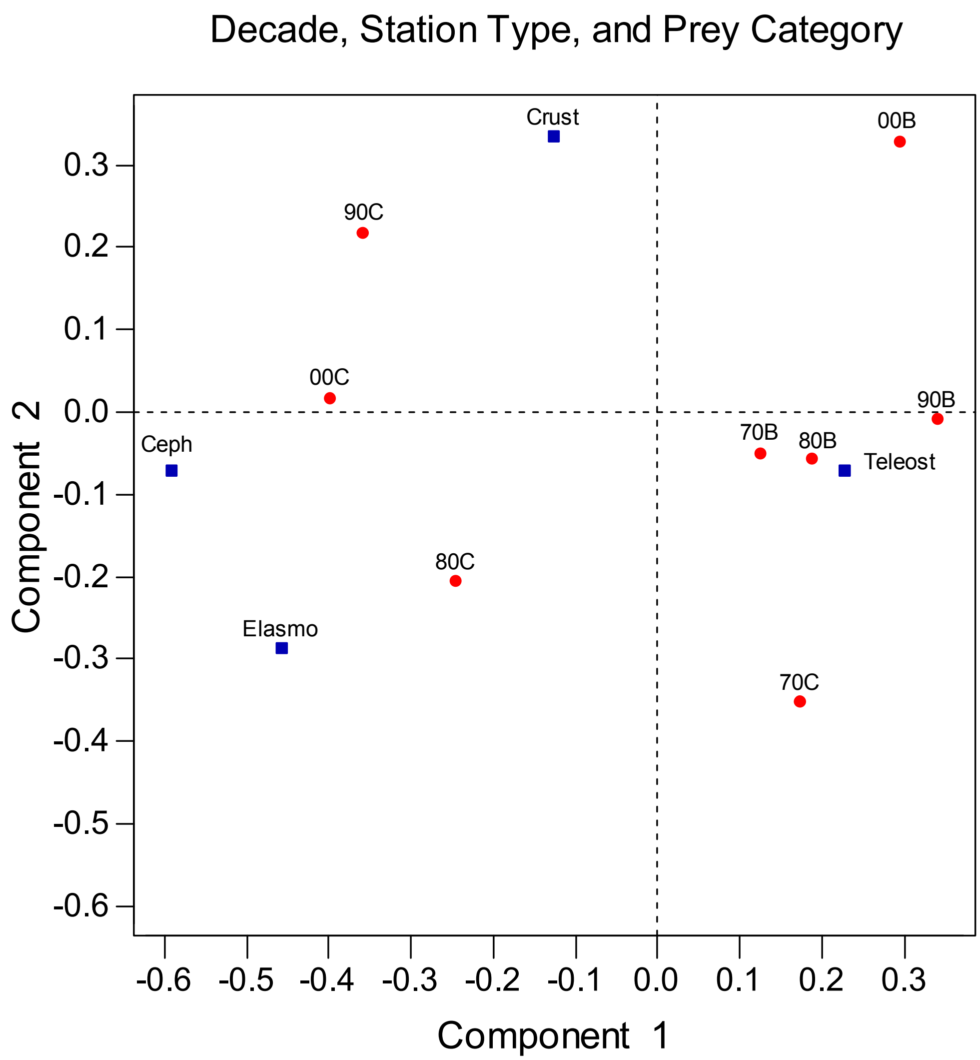
The effect of location (Bay versus Coastal) and decade (1970s, 1980s, 1990s, and 2001-2002) on prey categories was examined using CA (Figure 25). No obvious trends emerged, particularly after removing the unknowns, the majority of which were from 2001-2002 (Figure 26). Coastal sites for all decades remained relatively close on PC1, as did Bay sites.

Figure 25: Biplot of decade (70 = 1970s, 80 = 1980s, 90 = 1990s, and 00 = 2000s), station type (B = Bay and C = Coastal), and prey group (teleost, crustacean, cephalopod, elasmobranch, and unknown) principal components (PCs) for component 1 and component 2 of a correspondence analysis using %F data.



Decade, Station Type, and Prey Category
Component 2
Component 1
1.0
0.5
0.0
0.0
0.5
1.0
00B
Crust
Unk
90B
Teleost
00C
90C
80B
70B
70C
Ceph
80C
Elasmo

Figure 26: Biplot of decade (70 = 1970s, 80 = 1980s, 90 = 1990s, and 00 = 2000s), station type (B = Bay and C = Coastal), and prey group (teleost, crustacean, cephalopod, and elasmobranch) principal components (PCs) for component 1 and component 2 of a correspondence analysis using %F data with unknown prey group eliminated.



Decade, Station Type, and Prey Category
Crust
00B
90C
00C
90B
Ceph
70B
80B
Teleost
80C
Elasmo
70C
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
-0.6 -0.5 -0.4 -0.3 -0.2 -0.1 0.0 0.1 0.2 0.3
Component 1
Component 2

DISCUSSION

The sandbar shark feeds on a wide variety of fishes and crustaceans, as well as elasmobranchs and cephalopods. Although one prey item, the mantis shrimp, had high IRI values for most size classes in the 2001-2002 samples, no single prey item occurred in more than 50% of stomachs from the entire data set, which suggests that this species is a generalist predator.

The abundance of unidentified teleosts in this diet study was due in part to how sorting and weighing of prey items were conducted. Pieces of flesh which could not be assigned to an identified prey item in the stomach were labeled as "unidentified" and weighed and counted separately. Many of these unidentified teleosts are probably represented by the species listed; however, given the diversity of fishes consumed, there are likely some other species in the "unidentified" category. Catching hungry sharks can also render identification difficult due to the advanced digestion stage of the items present in the gut, and samples obtained with longlines are more likely to be from hungry sharks with empty or almost empty stomachs (Medved et al. 1985). Digestive action made it difficult to tell if crabs found in the stomachs were molting or "soft crabs". The low pH of sandbar shark stomachs, which has been measured at approximately 1.8, makes the stomach a very effective area for digestion (Y. Papastamatiou, pers. comm.). Enzyme activity may also play a role. Some elasmobranchs such as *Squalus acanthias* utilize chitinolytic enzymes to speed crustacean digestion (Fänge et al. 1979), but it is not yet known if sandbar sharks have this enzyme.

Weights of prey items may also have been influenced by method of capture. Medved et al. (1985) found that the mean total weight of food items found in sandbar sharks captured using longline gear was significantly less than the weight of food items from sandbar sharks caught in gillnets. Because over half of the samples from this study were obtained using longline gear, the percent weight and, consequently, the percent IRI values calculated in this study may be an underestimate. If possible, it is preferable to use gillnets to obtain sharks for use in diet studies.

The large number of fish families (28) consumed by the sharks in this study is a reflection of the diversity of habitat and fauna present in Chesapeake Bay and surrounding waters. Two of the fishes found most frequently in sandbar shark stomachs are hogchoker and croaker, which were the second and fourth most abundant finfish species captured by the VIMS Trawl Survey from May through October, 2002 (VIMS 2003). The types of fishes found in sandbar shark stomachs also reflect habitat usage by the shark. Tracking studies indicate that while in Chesapeake Bay *C. plumbeus* spends significant amounts of time at least three meters above the bottom (Grubbs 2001). The data presented here suggest, as do Medved et al. (1985)'s and Stillwell and Kohler (1993)'s, that sandbar sharks feed on mostly demersal species (e.g., croaker and hogchoker) but do make forays into the water column, as seen by the presence of mid-water fishes in the diet (e.g., menhaden and bluefish). This increased utilization of the water column occurs mostly at night, and sandbar sharks have been observed at the mouths of tidal creeks near large aggregations of menhaden and croaker (Grubbs 2001). The sharks may be attracted to similar aggregations of crustaceans. Surface swarming of mantis shrimp has been reported in Narragansett Bay and in the Gulf of Aden (McCluskey 1977), although this behavior has not yet been explained and has not been reported in Chesapeake Bay. Other types of prey—gastropods, bivalves, and other benthic organisms—appear infrequently in the diet and are likely incidentally consumed.

In terms of diet overlap, juvenile and neonate males and females appear to use the nursery habitat in the same way, with no apparent difference in diet. Stillwell and Kohler (1993) noticed some differences in diet between nearshore males and females which may have been due to segregation by sex or to sampling location. Comparison of diet by sex for larger juveniles and adults was not possible in this study due to the small number of males captured. This is not unusual. Sex segregation is evident in mature sandbar sharks (Springer 1960), and larger males are infrequently encountered at the stations fished by the VIMS Shark Ecology Program. Of 631 sharks with precaudal lengths greater than 100 cm that were caught by the project, only 53 were male.

Sandbar sharks undergo clear ontogenetic changes in diet, with elasmobranchs and cephalopods increasing in importance with shark size and crustaceans decreasing in importance. Teleosts remain a staple throughout the lifespan; however, types and sizes of fishes consumed may change. While Shannon-Wiener prey diversity index values indicate that larger animals feed on more diverse prey, the list of prey species for each size class suggests that smaller sharks eat more species. The larger sharks are in fact feeding more evenly among prey groups, while the smaller sharks are taking a wider variety within those categories. These ontogenetic changes in diet mostly reflect habitat use, although physiological and morphological constraints certainly play at least some role.

The frequent occurrence of crustaceans, particularly mantis shrimp, in juvenile sandbar shark diet is an indication of shared habitat preferences for predator and prey. *Squilla empusa* prefers deep (10-20 m) areas with high salinities (VIMS 2002). Tracking studies indicate that juvenile sandbar sharks frequent the deep, saline (> 20.5 parts per thousand) pockets of the bay (Grubbs 2001). What is available for forage in areas of this preferred salinity may vary by region. The neonates and juveniles in Medved et al.'s (1985) study in Chincoteague showed a clear preference for blue crab, whereas overall numbers for this study suggest that mantis shrimp is more frequently consumed. This difference in diet is likely due to regional habitat use, with more portunid crabs consumed in the Wachapreague region and more mantis shrimp consumed in the Sand Shoal Inlet region; Machipongo serves as a transitional region, with values in between.

After preliminary attempts to sample in Chincoteague, in which only one sandbar shark was caught in 20 gillnet sets, sampling in Chincoteague was deemed cost and time ineffective. Due to the lack of Chincoteague samples, direct comparisons between present and past data for juvenile diet cannot be made, and it is uncertain whether blue crab abundance and time played a role in the differing results of these two studies. The most likely scenario, however, is that diet varies between the regions. This conclusion is borne out by the importance of fish to the Bay juveniles and neonates and the importance of crustaceans to the sharks in the Eastern Shore nursery. If juvenile sharks frequently move between Eastern Shore regions or between Eastern Shore and the lower Bay, interregional differences in diet may be difficult to confirm. However, juvenile sharks tracked in lower Chesapeake Bay did not leave that region in 50 hours (Grubbs 2001), so frequent Bay to Eastern Shore movements are unlikely. Current efforts to monitor movements of sharks in Eastern Shore waters should shed light on home ranges in that area.

Teleosts are the most important prey item of sharks in size classes II and III. The diets of sharks between 60 and 100 cm PCL show a transition from crustacean dominance to fish and elasmobranch dominance. Frequency data show continued importance of crustaceans: mantis shrimp are still consumed very frequently by class II, but with decreasing regularity in class III. However, with increasing shark size, weight of prey items begins to become more important, and crustaceans are less important by weight. The increase in teleost prey may also reflect an increased use of coastal waters. Classes II and III have a high degree of dietary overlap, but the differences in importance of crustaceans and elasmobranchs between the two diets argue against lumping the two classes together.

Larger sandbar sharks spend more time in deeper coastal waters and thus are likely to encounter more cephalopods and more elasmobranchs. Salini et al. (1992) noted that Australian *Carcharhinus amblyrhynchos* and *Carcharhinus sorrah* both consumed more cephalopods at offshore sites than at estuarine sites. The trend toward increased use of larger prey items (e.g., elasmobranchs) with increased size is seen in many sharks, including the Galapagos shark, *Carcharhinus galapagensis* (Wetherbee et al. 1996) and the tiger shark (Lowe et al. 1996). Incorporation of larger, heavier prey items is an energetic benefit, giving the predator more return on its energetic investment (search and capture) (Labropoulou et al. 1999). Regional differences in diet for the larger sharks are suggested by the differences in diet between stations and station types but cannot be detected with any certainty due to small sample sizes.

The non-significant results from the MANOVA suggest that there are no detectable significant effects of station, shark size, or both on prey choice. This apparent contradiction of correspondence analysis and chi-squared test results is likely due to a small sample size. The creation of station type subsets within size class subsets of data lead to inconclusive results. Based on the correspondence analysis and chi-squared tests performed in this study, location and shark size do appear to influence the prey types comprising sandbar shark diet. The analysis of juvenile diet within the Eastern Shore sites suggests that location may affect diet within a size class. If more samples were obtained, the interactions of these two factors would become clear.

This study formed four main conclusions about sandbar shark diet:

1) Ontogenetic changes in diet were observed, with increasing incorporation of elasmobranchs and cephalopods in diet with size and decreasing predation on crustaceans.
2) Juvenile diet varied between nursery ground regions. Teleosts were consumed more frequently in the lower Bay, and crustaceans were consumed more frequently on the Eastern Shore.
3) Juvenile diet varied within regions of the Eastern Shore, with increasing portunid crab consumption in the northernmost region of the study (Wachapreague) and more mantis shrimp consumption in Sand Shoal Inlet.
4) Effects of time on diet must be tested within the activity space of the shark to minimize biases due to location.

Ongoing tracking studies on the Eastern Shore should reveal more about behavioral patterns of sandbar sharks in this ecosystem compared to the lower Bay. Other future studies might involve prey handling and selectivity experiments. This study shows that *Carcharhinus plumbeus* has very diverse prey base. As a generalist, it is unlikely to strongly impact the population of any particular species, and in turn is not likely to be strongly affected by fluctuations in abundance of a single prey species. The diversity of items within each prey category attests to the sandbar shark’s ability to sample new prey and confirms its versatility as a predator.

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VITA

Julia Ellis

Born in La Jolla, California on September 27, 1974. Graduated from Hudson High School (Hudson, Ohio) in 1992. Earned B.S. in biology from the College of William and Mary in 1996. Entered the Master of Science program at the College of William and Mary's School of Marine Science in August 2000.